



## First record of the littoral genus *Alismobates* (Acari: Oribatida) from the Atlantic ocean, with a redefinition of the family Fortuyniidae based on adult and juvenile morphology

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### Abstract

*Alismobates inexpectatus* sp.n., found on rocky shores of the archipelago of Bermuda is described from larva to adult. Additionally a detailed description of the immatures of *Fortuynia atlantica*, also known from Bermuda, is given. Based on adult and juvenile morphology the position of the genus *Alismobates* within the family of Fortuyniidae is clearly confirmed. Furthermore the definition of the family Fortuyniidae is revised and the classification of its members is discussed. The Fortuyniidae are best characterized by the presence of a “van der Hammen’s Organ”, whereas the configuration of cuticular channels differs remarkably between the genera *Fortuynia* and *Alismobates*. The juveniles of *A. inexpectatus* and *F. atlantica* Krisper et Schuster, 2008 exhibit conformity in most aspects, whereas porose areas associated with notogastral setae and singular pores in the lateral and posterior ventral folds leading into fine tracheal tubes are documented for the first time in fortuyniid immatures. These pores are part of a complex plastron system expressed in immatures to withstand tidal inundation. The present discovery of *Alismobates inexpectatus* is the first record of a member of this genus from Atlantic coasts and therefore represents a considerable extension of the geographic distribution of this taxon.

**Key words:** Bermuda, *Alismobates inexpectatus*, *Fortuynia atlantica*, biogeography, thalassobiontic

### Introduction

The family of Fortuyniidae belongs to a small group of thalassobiontic oribatid mites that have managed to colonize intertidal habitats of rocky shores, boulder beaches and mangrove forests, leading a life on the edge of two daily colliding environments. At present the Fortuyniidae are consisting of three genera, *Fortuynia* van der Hammen, 1960, *Alismobates* Luxton, 1992 and *Circellobates* Luxton, 1992, and show a transoceanic distribution along shores of tropical and subtropical areas (Schuster 1989; Krisper & Schuster 2008). The majority of these species is

confined within the Indo-Pacific region (Procheş & Marshall 2001; Marshall & Pugh 2002; Bayartogtokh *et al.* 2009), whereas prior to the present study, *Fortuynia atlantica* Krisper et Schuster, 2008, found on the archipelago of Bermuda (Krisper & Schuster 2008), represented the sole record of a fortuyniid species from Atlantic coasts.

The family of Fortuyniidae is taxonomically well delimited against closely related families, such as the Seleuribatidae, Ameronothridae or Tegeocranellidae (e.g. Luxton 1967; Grandjean 1966, 1968; Weigmann & Schulte 1977; Behan-Pelletier 1997), but its systematic definition is mainly based on the morphology of the diverse genus *Fortuynia*, at present including ten species and two subspecies. The other two genera, *Alismobates*, with only two species, and the monotypic *Circellobates* are known to a far lesser extent and existing literature about these taxa is scarce (Luxton 1992; Karasawa & Aoki 2005). Luxton (1992) established the latter two genera but gave no definite reason for the placement of these within the Fortuyniidae. Karasawa and Aoki (2005) published a valuable redescription of *A. reticulatus* Luxton, 1992 but also missed to highlight characteristics justifying this species as a valid member of the family Fortuyniidae. Continuative literature is lacking and therefore the systematic positions of the genera *Alismobates* and *Circellobates* within this family remained more or less uncertain.

The taxonomic history of Fortuyniidae is one of the best examples for the importance of juvenile morphology in systematic considerations. Based on the discovery of immatures of *Fortuynia yunker* van der Hammen, 1963, the taxon was removed from its erroneous position within the Podacaridae and given family status (van der Hammen 1963). Nevertheless, since then the ontogenetic aspect has been largely neglected and thus only the immatures of four out of thirteen described fortuyniid species are known yet.

## Material and methods

**Collection:** Specimens examined in the present study were collected in different years from rocky shores of the Bermuda archipelago. Samples of algae were removed from rocks in the intertidal zone and afterwards put in a Berlese-Tullgren apparatus for the extraction of the littoral mites.

Sample localities of specimens used for morphological analysis:

*Alismobates inexpectatus* n.sp.: (a) Tobacco Bay, 17/7/1981 (Be-108, R. Schuster leg.); *Bostrychia tenella* on rocks, 32°23'18''N 64°40'41''W, 12/8/2011 (Be-06-TP, T. Pfingstl leg.). (b) Whalebone Bay, 01/08/1981 (Be-164, R. Schuster leg.). (c) Devonshire Bay, 15/9/1981 (Be-268, R. Schuster leg.).

*Fortuynia atlantica*: (d) Concrete Beach near BIOS Station, *Bostrychia tenella* on rocks, 32°22'10''N 64°41'50''W, 25/8/2011 (Be-19-TP, T. Pfingstl leg.). (e) Gunner Bay, *Bostrychia tenella* on rocks, 32°22'19.54''N 64°39'07.09''W, 11/9/2011 (Be-30-TP, T. Pfingstl leg.).

**Preparation:** For investigation in transmitted light all specimens were stored in ethanol (70% or absolute ethanol), then heated in lactic acid (80°C for about 20 minutes) and afterwards embedded in BERLESE mountant. Observations, drawings and photographs were made with an Olympus BH-2 Microscope as well as with a WILD HEERBRUGG M20, both equipped with a drawing attachment. Image stacks were obtained by an Olympus Camedia C4040 zoom digital camera and layered with the Combine ZP software.

## Results

### Redefinition of the family Fortuyniidae van der Hammen, 1963

Thalassobiontic pycnonotic Brachypylina. Immatures plicate, smooth centrodorsal area, laterally and ventrally large folds. Larva bideficient, seta *h*<sub>3</sub> absent or vestigial; nymphs unideficient. Palptarsal solenidion not on apophysis and not associated with *acm*. Tutorium absent or present. Pedotecta I and II present, weakly developed. Lateral system of cuticular channels ("van der Hammen's Organ") present. Dorsosejugal suture complete. Lenticulus present or absent. Notogastral setation 14 pairs, *c*<sub>3</sub> absent or vestigial. Epimeral setation 3-1-2-2 or 3-1-3-2 or 3-1-2-3 or 3-1-3-3. Genital and anal plates large, closely adjacent. Genital setation 4-5 pairs of setae. Three pairs of adanal setae. Two pairs of anal seta. Lyrifissure *iad* beside or posterior to *ad*<sub>2</sub>. Legs monodactylous, non-uniformly sclerotized. DDC *el* = seta *d* associated with solenidia on tibiae and genua absent in all stages (Grandjean 1954). Porose areas on all femora and trochanters III and IV present.

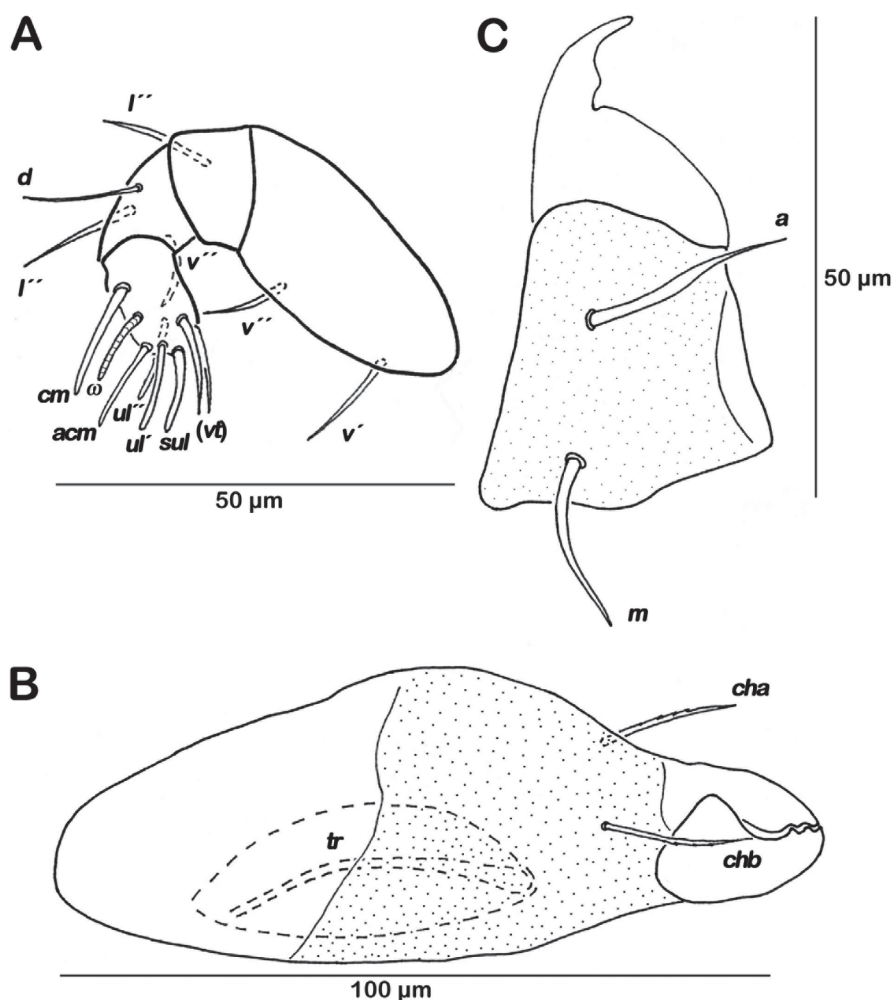
## Genus *Alismobates* Luxton, 1992

Medium sized (290µm–400µm body length) dark sclerotized intertidal mites. Interlamellar setae vestigial or short. Convergent lamellar ridges. Translamellar ridge demarcating rostrum. Sensillus clavate, spinose. Tutorium present. Van der Hammen's organ with specific anterior ventral channel. Pedotecta present, weakly developed. Lenticulus present. Notogaster with 14 pairs of setae. Pairs of single pores present on notogaster. Epimeral setation 3-1-2-2. Genital setae 4 pairs. Aggenital 1, adanal 3 and anal 2 pairs of setae.

### *Alismobates inexpectatus* sp. nov.

Type material - Holotype: female, Bermuda, Tobacco Bay, upper intertidal zone, rocks covered with mats of algae; 17/07/1981, R. Schuster leg. (Be-108=sample number in the collection R.S.). Paratypes: 4 females and 4 males, same locality as holotype. Deposition of holo- and paratypes: Senckenberg Museum für Naturkunde Görlitz, Germany (Collection Nr. 81/47300).

**Etymology.** About 30 years ago, when he discovered *F. atlantica* on Bermuda (Krisper & Schuster 2008), Schuster also collected specimens of another unknown species. He regarded these specimens to be individuals of a new selenoribatid species but did not pay further attention to it as he focused on the sexually dimorphic *F. atlantica*. Decades later, when Schuster was told that he had found at that time a new *Alismobates* species, he was very surprised. He did not expect a further fortuyniid species to be present on the archipelago of Bermuda, therefore the name refers to the Latin word “inexpectatus” meaning unexpected.



**FIGURE 1.** *Alismobates inexpectatus* adult. A) right pedipalp paraxial view. B) right chelicera paraxial view. C) right rutellum ventral view.

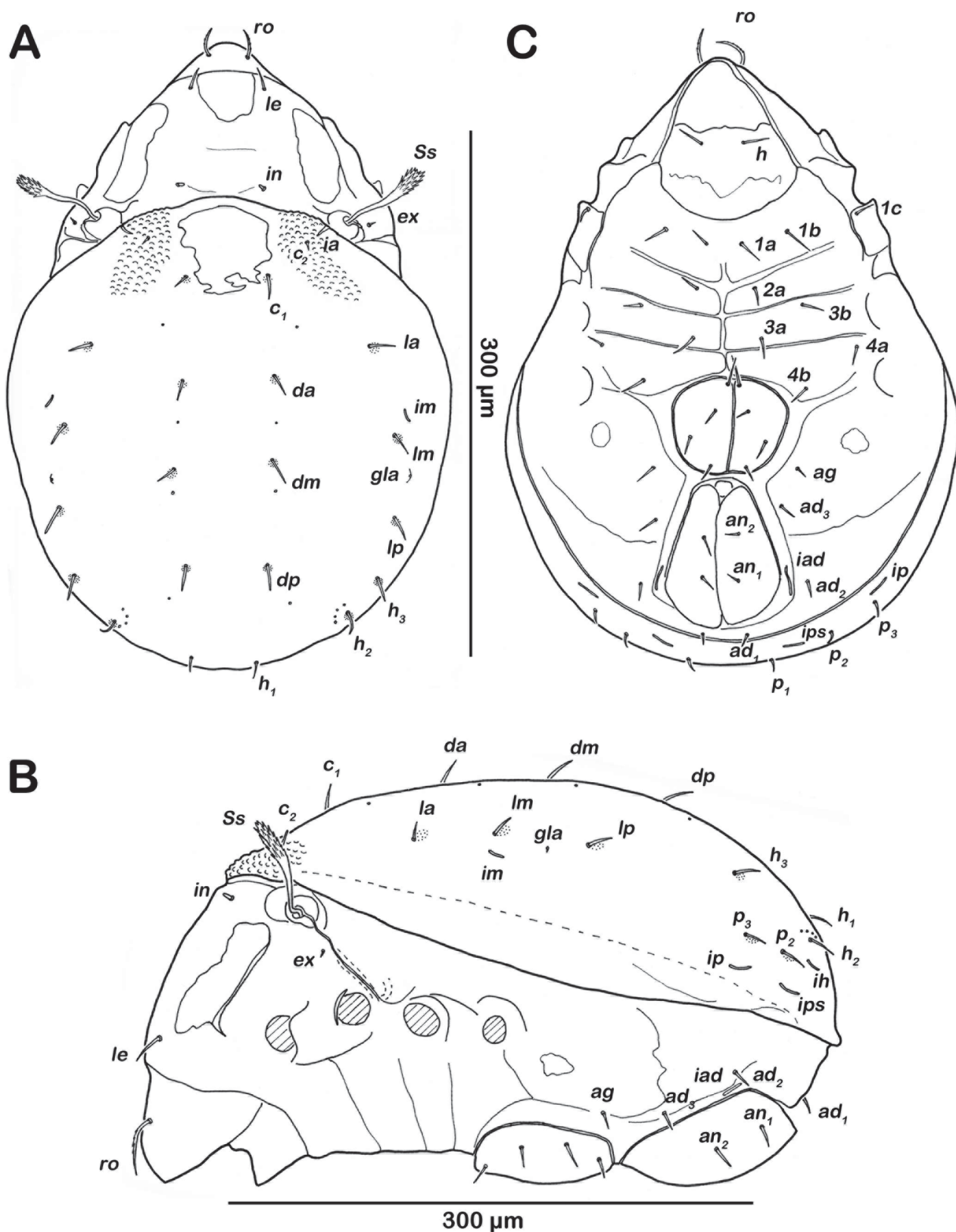
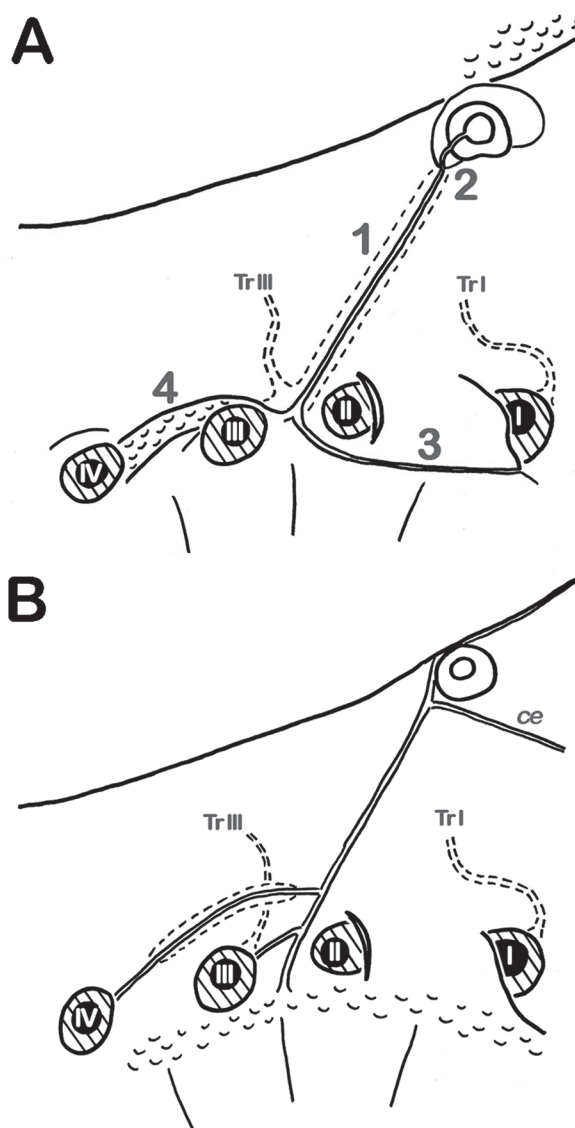


FIGURE 2. *A. inexpectatus* adult. A) dorsal view. B) lateral view. C) ventral view.

**Diagnosis.** Dark brown sclerotized mites. Habitus typical for the genus *Alismobates*. Average length 366 µm, mean width 246 µm. Notogaster oval in shape. No conspicuous sexual dimorphism in notogastral setation, porose areas, anogenital region and features of the legs; there is only the common sexual dimorphism in overall body size, with females being generally slightly larger. Van der Hammen's Organ well developed, but diverging from



*Fortuynia* typical pattern. Sensillus clavate, spinose. One pair of large cuticular ridges in position of prodorsal lamellae. Interlamellar setae minute. Lenticulus large, variable in shape. Areas flanking lenticulus conspicuously granular. Fourteen pairs of short and simple, notogastral setae, associated with small porose areas. Four pairs of single pores medially on notogaster and one pair of four semicircular grouped pores on posterior gastronic region. Epimeral setation 3-1-2-2. Four pairs of genital setae. One pair of aggenital setae. Three pairs of adanal setae. Two pairs of anal setae. Legs monodactylous with large claw. Porose areas on trochanters III and IV and all femora. Leg setation (chaetome, solenidia): Leg I 0-4-2-3-18, 1-2-2; leg II 0-4-2-3-15, 1-1-1; leg III 1-3-1-3-15, 1-1-0; leg IV 1-2-2-3-12, 0-1-0. Juveniles plicate with large foveate centrodorsal plate.



**FIGURE 3.** Schematic illustration of van der Hammen's organ. A) *Alismobates inexpectatus*. B) *Fortuynia* typical configuration. Arabic numbers refer to described parts in the text, Latin numbers refer to leg segments, lined areas represent leg acetabula, Tr I = acetabular trachea I and Tr III = acetabular trachea III.

**Description of adult.** Females (N=17), length: 360–391 µm (mean 375 µm), width: 240–253 µm (mean 249 µm); males (N=21), length: 347–372 µm (mean 356 µm), width: 235–249 µm (mean 242 µm)

**Integument.** Colour ranging from dark brown to nearly black. Cuticle appears shiny, but finely granulate under dissecting microscope.

**Prodorsum.** Cerotegument finely granular, larger granules next to anterior notogastral border. Rostrum rounded in dorsal view, but slightly projecting anteroventrally in lateral view. Whole rostrum clearly demarcated from remainder of prodorsum by an obvious transverse ridge. A pair of two slightly converging, thickened and

broad cuticular ridges in position of prodorsal lamellae. Borders of these ridges shaped irregularly except for lateral aspects showing a clear straight edge. A further single and nearly elliptic median area of thickened cuticle between lamellar setae. Rostral setae (*ro*) strong, simple and dorsally slightly barbed. Lamellar setae (*le*) simple, short and smooth. Interlamellar setae (*in*) minute. One pair of very short and fine exobothridial setae (*ex*). Bothridia cup-like with a lateral incision, strongly projecting, orifice narrow and circular. Sensilla of normal length, slightly clavate, distally spinose. An elliptic plate-like cuticular ridge dorsally adjacent to base of bothridium, covering dorsosejugal suture over a short distance.

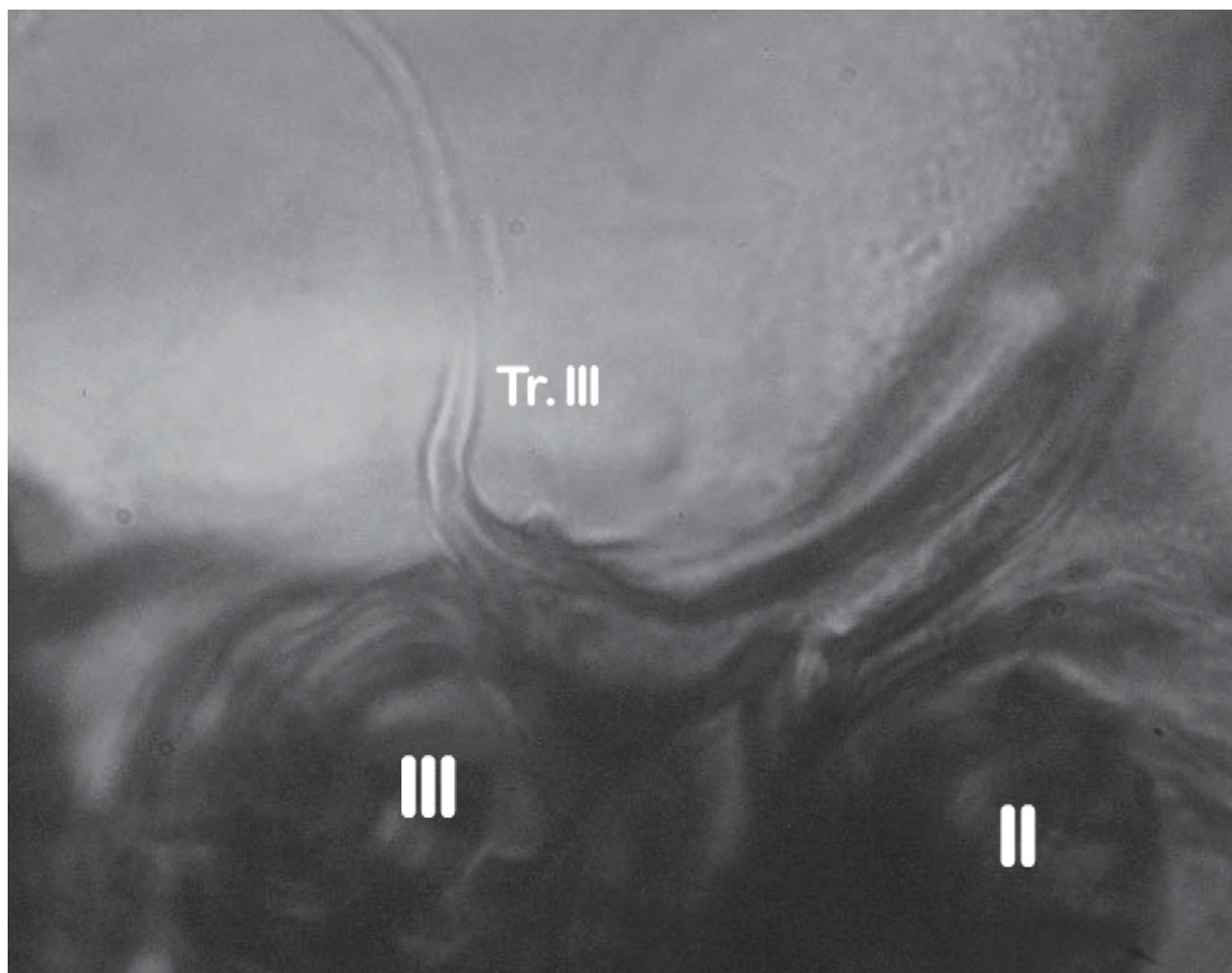
Gnathosoma. Pedipalp (Figure 1A) pentamerous 0-2-1-3-9 (including solenidion), trochanter very short, femur by far longest segment, genu, tibia and tarsus of almost equal length. Solenidion  $\omega$  on palptarsus erect, not associated with eupathidium *acm*. Chelicerae (Figure 1B) chelate, mobile digit slightly darker sclerotized, with three small, blunt but distinct teeth, whereas from frontal view most distal teeth split into two symmetrical teeth; fixed digit with two teeth, all teeth interlocking. Large lateral porose area from middle of chelicerae to joint of digits. Seta *cha* and *chb* of approximately the same length, both dorsally slightly pectinate. Trachea reaching into anterior part of chelicera. Gena well sclerotized but finely porose. Distal part of rutellum developed as thin triangular slightly curved inward membrane (Figure 1C). Seta *a* and *m* long, robust and smooth. Mentum regular, seta *h* simple, thin and of normal length.

Gastronotic region (Figure 2A). Conspicuously rounded, anterior notogastral margin distinct. Cerotegument mainly finely granular, but showing conspicuously larger granules in areas flanking median light spot. Lenticulus developed as large anterior median light spot with irregular borders. Shape of lenticulus highly variable, from rectangular to square. Fourteen pairs of relatively short and simple notogastral setae,  $c_{1-2}$ , *da*, *dm*, *dp*, *la*, *lm*, *lp*,  $h_{1-3}$ ,  $p_{1-3}$ ; seta  $c_3$  absent. Small circular porose areas associated with bases of all notogastral setae. Additionally four pairs of single pores arranged in two median parallel rows. First pair posterior  $c_1$ , second posterior *da*, third posterior *dm* and fourth posterior *dp*. Next to seta  $h_2$  a series of four pores arranged in a semicircular median row. No difference in the arrangement of these pores between the sexes. Five pairs of notogastral lyrifissures present; *ia* next to seta  $c_2$  close and rectangular to anterior notogastral border; *im* slightly anterior and laterad of seta *lm*; *ih* between seta  $h_2$  and  $h_1$ ; lyrifissures *ip* and *ips* laterally of seta  $p_3$  and  $p_2$  respectively. Orifice of opisthonotal gland (*gla*) laterally between setae *lm* and *lp*.

Lateral aspect (Figure 2B). Cerotegument generally finely granular, larger granules in areas surrounding acetabula. Tutorium present, anterior part a ventrad curved bulge, posterior part fused with prodorsal lateral ridge. Pedotectum I weakly developed, only slightly projecting. Pedotectum II a minute plate-like ridge. Discidium not conspicuously expressed. Van der Hammen's Organ modified, consisting of a system of four combined parts (Figure 3A): First and major part (1), a large canal connected with the outside only by a small slit, starts at the lateral part of dorsosejugal suture, passes posterior of bothridium and runs ventrad to area between acetabulum II and III, where it diverges into an anterior and posterior branch. Second and smallest part (2) consisting of a short channel connecting lateral incision of bothridium with the above mentioned main canal. Third part (3) is the anterior lateroventral branch passing acetabulum II posteriorly and curving on the ventral side anteriorly into a distinct longitudinal canal reaching ventral tip of pedotectum I where it opens in acetabulum I. Fourth part (4) is the posterior branch, represented by a deepened broad groove running caudad passing dorsally acetabulum III and ending at acetabulum IV. Stigma of acetabular trachea III situated in ramification of part one, three and four (Figure 4).

Ventral region of idiosoma (Figure 2C). Cerotegument in sternal region finely granular, larger granules laterally next to acetabula and on most posterior part of ventral plate. Epimeral setation 3-1-2-2, all setae simple and smooth. Seta *Ib* about a third longer than other setae. Seta *Ic* close to pedotectum I, laterad of ventral longitudinal channel of van der Hammen's Organ. Internal borders of all epimera well visible, sternal apodemes II, III and IV well developed. Genital and anal opening closely adjacent, both surrounded by strongly sclerotized cuticle. Rounded genital plates with four pairs of fine and simple genital setae. First and longest pair near medial margin of valves, second and fourth pair median on plates and third pair close to lateral margin of valves. Laterad of genital opening a circular spot of thickened cuticle. One pair of simple aggenital setae *ag*. Anal valves nearly triangular, median margins slightly overlapping. Outer part of preanal organ triangular with rounded edges, inner part shaped like a broad transverse bar. Two pairs of short and simple anal setae,  $an_{1-2}$ , arranged in a longitudinal row. Three pairs of short and simple adanal setae,  $ad_3$  laterad of anterior third of anal plates,  $ad_2$  near posterior third of anal valves and  $ad_1$  posterior of anal opening. Lyrifissure *iad* orientated longitudinally and flanking posterior third of

anal plates. Thickened cuticle on posterior part of ventral plate, clearly delimited from anterior thinner cuticle by two concave symmetric arches next to anal opening.



**FIGURE 4.** *A. inexpectatus* micrograph showing origin of acetabular trachea III. Latin numbers refer to leg segments.

Legs (Figure 5). Monodactylous. Long, strong hook-like claws. Cuticle heterogeneous, trochanters dark, proximal third of femur I and II light remainder dark, femora III and IV dark, all genua dark, all tibiae light and proximal part of all tarsi only slightly darker than distal part. Femora without ventral carina. Cerotegument generally finely granular, larger granules only on distal third of all femora. All tarsi with proximal lyrifissure. Large irregularly shaped porose areas on ventral paraxial side of femur I and II, porose areas on proximal part of femora III and IV divided in a large dorsal and a smaller ventral part, kidney-shaped porose areas on paraxial dorsal aspect of trochanters III and IV. Dorsal seta *d* on all femora slightly thickened and dorsally serrate. Lateral setae of all genua short, broadened and slightly serrate. Ventral setae of all tibiae and tarsi, long and ventrally strongly serrate. Solenidia  $\phi_{1-2}$  on tibia I borne on small apophysis. Chaetome and solenidia see table 1.

**Common features of juvenile stages.** Apherodermous. Colour dark brown. Integument plicate and soft, except for centrodorsal plate (Figure 6). Prodorsum triangular, anterior part finely granular, rostrum rounded. Rostral (*ro*) and lamellar setae (*le*) short and simple. One pair of short exobothridial setae (*ex*) and minute interlamellar setae (*in*). Sensilla of normal length clavate and distally spinose. Bothridia cup-like, laterally opened. Medially on posterior border of prodorsum groups of distinct pores leading into fine tracheal tubes (Figure 7A); these structures are difficult to detect as in dorsal view they are hidden beneath anterior folds of gastronomic region. Gnathosoma no obvious differences to adult stage. Hysterosoma slightly convex. Hysterosomal cupules not traceable in any stage. Large, foveate and stronger sclerotized centrodorsal plate bearing all notogastral setae, except for  $c_{1-3}$  in all stages and seta  $h_2$  in the larval stage. Lateral borders of plate straight, anterior border slightly convex, posterior border

strongly convex. In nymphal stages posterior part of this plate showing a median lesser sclerotized and slightly concave conspicuous area without foveae resembling an inverted Y. Two parallel longitudinal rows of slightly darker pigmented spots on centrodorsal plate, whereas these spots are hardly discernable in most of the specimens. Large folds framing centrodorsal plate completely, showing fine granular surface. Within the lateral folds at least four hardly discernable pores on a level with acetabulum III and a series of further pores (number is hard to determine) aligned longitudinally. Orifice of opisthonotal gland (*gla*) located in posterior third of lateral folds. Small circular or elliptic porose areas associated with bases of all notogastral setae. Ventral sejugal suture developed as distinct furrow, posterior border medially opened over a short distance. Integument surrounding anal area folded. In nymphal stages no distinct genital sclerites developed, genital opening only a thin longitudinal slit, inner margins showing small granules. Anterior to genital area a slightly rostrad arched large furrow showing conspicuous granules. Nymphs with two distinct slightly curved furrows posterior of genital area, reaching from acetabulum IV to anterior end of anal opening, where they pass into distinct folds framing anal orifice. Within these furrows posterior of genital opening, fine cuticular pores. Anal area conspicuously finely granular. Legs monodactylous. Dorsal setae of tibiae and genua absent when respective solenidion present. Solenidia on tibia I borne on small apophysis. Large porose areas on ventral paraxial side of femora I and II and on dorsal paraxial side on femora III and IV. Circular porose areas on paraxial dorsal side of trochanters III and IV.

**TABLE 1.** *Alismobates inexpectatus*. Chaetome and solenidia from larva to adult. First development of setae characterized by letters. ( ) = pairs of setae, - = no change with regard to preceding stage.

	Instars	Trochanter	Femur	Genu	Tibia	Tarsus	Chaetome	Solenidia
Leg I	larva	-	<i>d, bv''</i>	( <i>l</i> ), $\sigma$	( <i>l</i> ), $v', \varphi_1$	( <i>pl</i> ), ( <i>pv</i> ), <i>s</i> , ( <i>a</i> ), ( <i>u</i> ), ( <i>p</i> ), ( <i>tc</i> ), ( <i>ft</i> ), $\omega_1$	0-2-2-3-16	1-1-1
	protonymph	-	<i>l'</i>	-	-	$\omega_2$	0-3-2-3-16	1-1-2
	deutonymph	-	<i>l''</i>	-	$\varphi_2$	-	0-4-2-3-16	1-2-2
	tritonymph	-	-	-	-	( <i>it</i> )	0-4-2-3-18	1-2-2
	adult	-	-	-	-	-	0-4-2-3-18	1-2-2
Leg II	larva	-	<i>d, bv''</i>	( <i>l</i> ), $\sigma$	<i>l', v', \varphi</i>	( <i>pv</i> ), <i>s</i> , ( <i>a</i> ), ( <i>u</i> ), ( <i>p</i> ), ( <i>tc</i> ), ( <i>ft</i> ), $\omega$	0-2-2-2-13	1-1-1
	protonymph	-	<i>l'</i>	-	-	-	0-3-2-2-13	1-1-1
	deutonymph	-	<i>l''</i>	-	-	-	0-4-2-2-13	1-1-1
	tritonymph	-	-	-	<i>l''</i>	( <i>it</i> )	0-4-2-3-15	1-1-1
	adult	-	-	-	-	-	0-4-2-3-15	1-1-1
Leg III	larva	-	<i>d, ev'</i>	<i>l', \sigma</i>	$v', \varphi$	( <i>pv</i> ), <i>s</i> , ( <i>a</i> ), ( <i>u</i> ), ( <i>p</i> ), ( <i>tc</i> ), ( <i>ft</i> )	0-2-1-1-13	1-1-0
	protonymph	-	-	-	-	-	0-2-1-1-13	1-1-0
	deutonymph	$v'$	-	-	-	-	1-2-1-1-13	1-1-0
	tritonymph	-	-	-	-	( <i>it</i> )	1-2-1-1-15	1-1-0
	adult	-	<i>l'</i>	-	( <i>l</i> )	-	1-3-1-3-15	1-1-0
Leg IV	protonymph	-	-	-	-	( <i>pv</i> ), ( <i>u</i> ), ( <i>p</i> ), <i>ft''</i>	0-0-0-0-7	0-0-0
	deutonymph	-	<i>d, ev'</i>	<i>d, l'</i>	$v', \varphi$	<i>s</i> , ( <i>a</i> ), ( <i>tc</i> )	0-2-2-1-12	0-1-0
	tritonymph	$v'$	-	-	-	-	1-2-2-1-12	0-1-0
	adult	-	-	-	( <i>l</i> )	-	1-2-2-3-12	0-1-0

**Larva.** Length (N=10): 160–197  $\mu$ m (mean 176  $\mu$ m)

Gastronotic region (Figure 8A). Eleven pairs of slightly thickened and slightly serrate notogastral setae;  $c_{1-3}$ , *da*, *dm*, *dp*, *la*, *lm*, *lp*,  $h_{1-2}$ ;  $h_3$  absent. Conspicuous transverse ridge on centrodorsal plate passing posterior line of setae *dm* and *lm*.

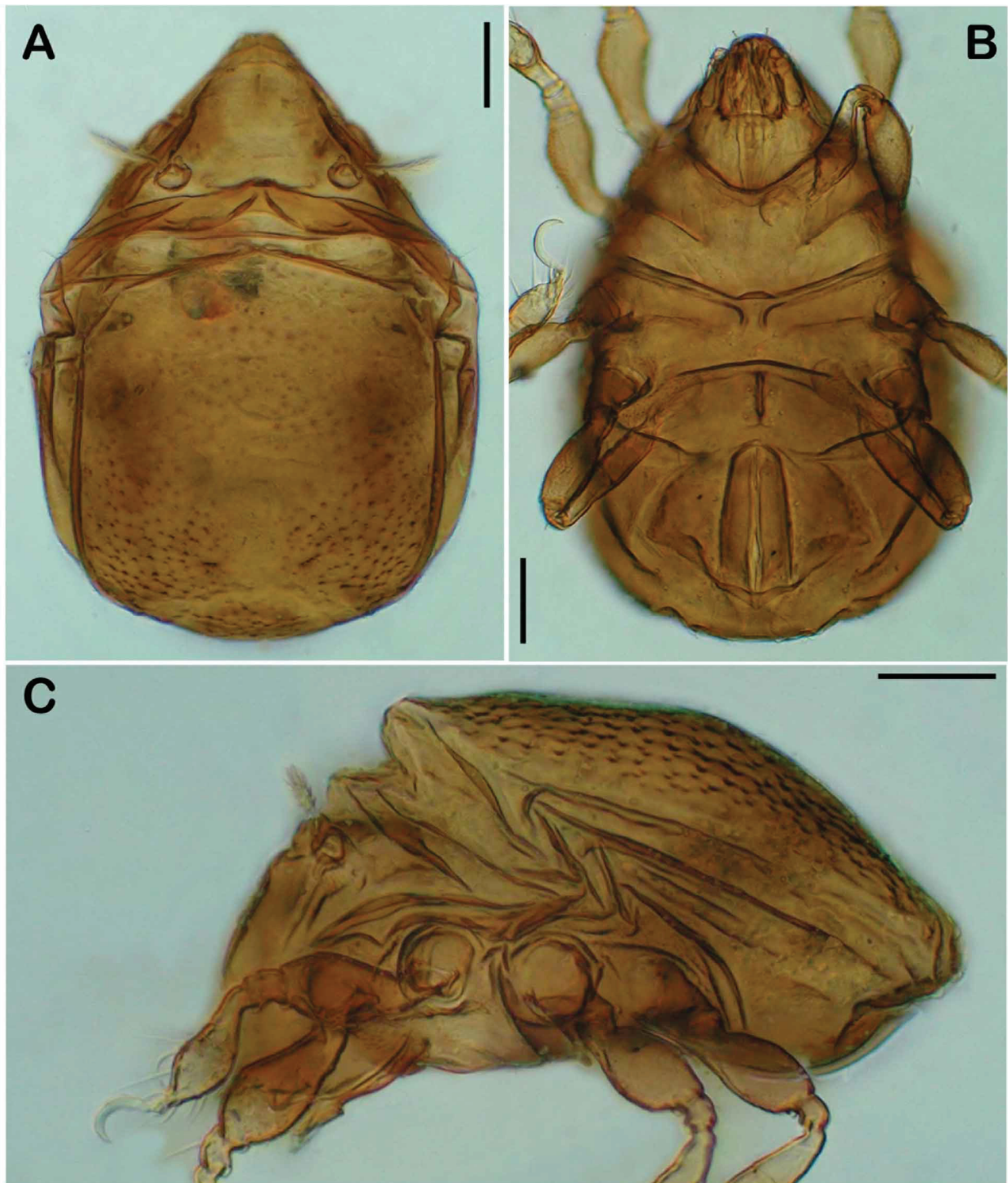
Ventral region of idiosoma (Figure 8B). Epimeral setation 3-1-2, epimeral setae of normal length, thin and simple, except for seta *1c* shaped valve-like protecting Claparède organ. Cuticle framing the latter anteromedially thickened and slightly projecting. Integument posterior of ventral sejugal furrow with a few inconspicuous transverse folds.

Legs. Setation and solenidia see table 1.









**FIGURE 6.** *A. inexpectatus* LM-micrographs. Scale bar: 50µm. A) deutonymph dorsal view, layered from 19 images. B) deutonymph ventral view, layered from 7 images. C) protonymph lateral view, layered from 21 images.

**Protonymph.** Length (N=24): 200–262 µm (mean 237 µm)

Gastronotic region (Figures 8C, 9). Fifteen pairs of notogastral setae;  $c_{1-3}$ ,  $da$ ,  $dm$ ,  $dp$ ,  $la$ ,  $lm$ ,  $lp$ ,  $h_{1-3}$  and  $p_{1-3}$ , all setae lesser thickened from this stage. Transverse ridge on centrodorsal plate passing posterior line of setae  $dm$  and  $lm$  absent from this stage.

Ventral region of idiosoma (Figure 8D). Epimeral setation 3-1-2-1. Seta  $1c$  developed as normal seta, next to trochanter I, seta  $4a$  close to trochanter IV. One pair of short genital setae. Aggenital setae absent.

Legs (Figure 10). Chaetome and solenidia see table 1.

**Deutonymph.** Length (N=31): 262–311 µm (mean 287 µm).

Gastronotic region (Figure 11A). Fifteen pairs of notogastral setae, same positions and shapes as in protonymph.

Ventral region of idiosoma (Figure 11B). Epimeral setation 3-1-2-1. Two pairs of short genital setae arranged in a longitudinal row. One pair of simple and short aggenital setae *ag*. Three pairs of adanal setae *ad*<sub>1-3</sub> flanking anal valves.

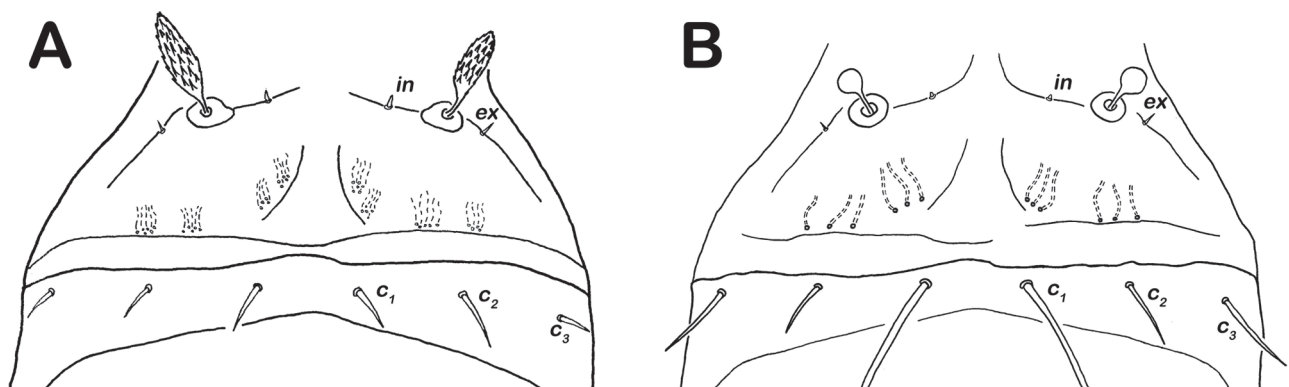
Legs (Figure 12). Chaetome and solenidia see table 1.

**Tritonymph.** Length (N=16): 329–386  $\mu\text{m}$  (mean 363  $\mu\text{m}$ )

Gastronotic region (Figure 11C). Fifteen pairs of notogastral setae, no difference to deutonymph.

Ventral region of idiosoma (Figure 11D). Epimeral setation 3-1-2-2, seta *4b* median on epimeral plate IV. Three pairs of short genital setae in a longitudinal row. One pair aggenital setae *ag*. Three pairs of adanal setae *ad*<sub>1-3</sub>. Two pairs of anal setae *an*<sub>1-2</sub>, sometimes asymmetrical variation with three setae developed on only one valve (as shown in Figure 11D).

Legs. Chaetome and solenidia see table 1.



**FIGURE 7.** Prodorsal pores in fortuyniid immatures. A) *Alismobates inexpectatus*. B) *Fortuynia atlantica*.

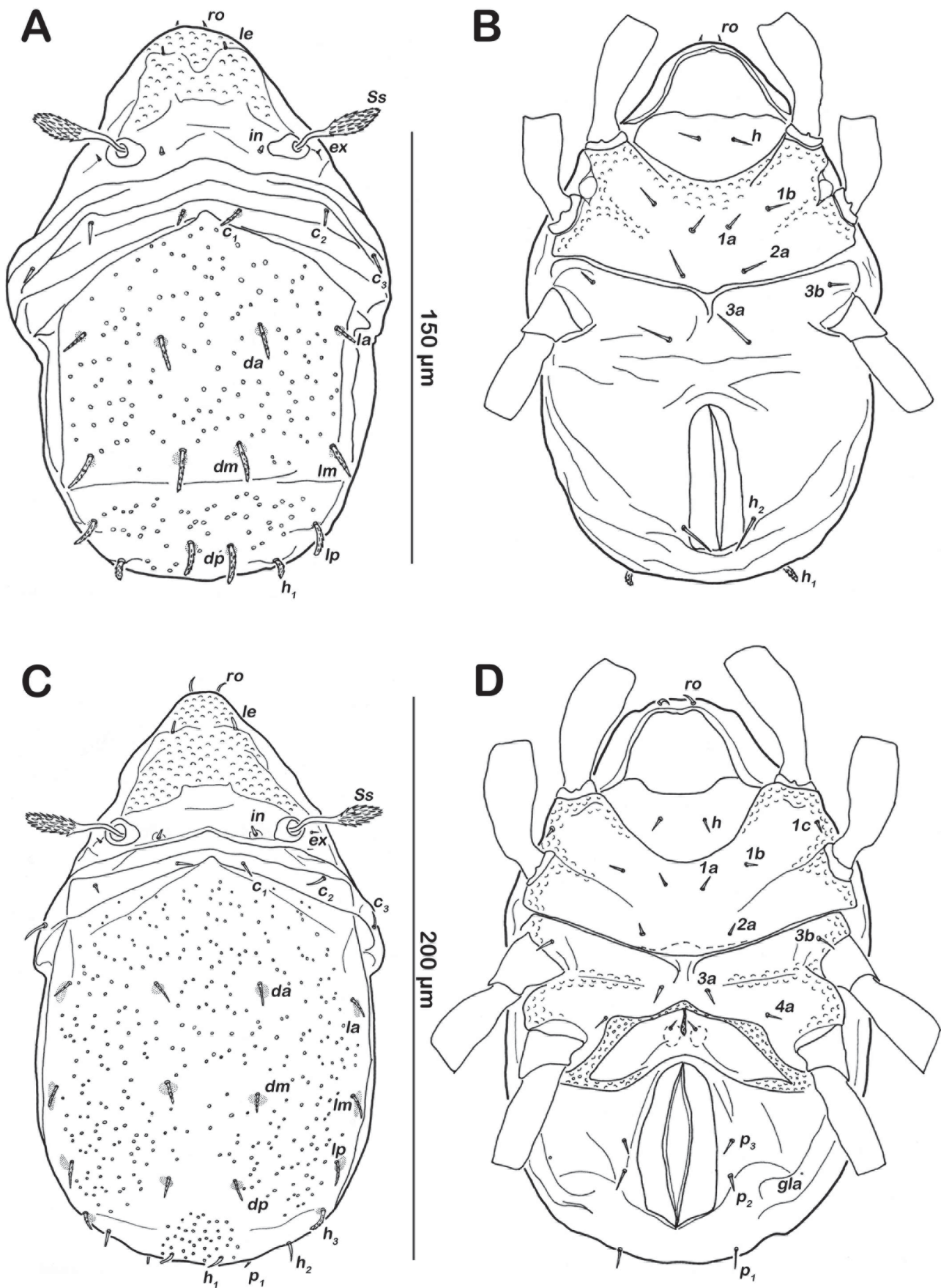
### Genus *Fortuynia* van der Hammen, 1960

Medium sized (400 $\mu\text{m}$ –600 $\mu\text{m}$  body length) dark sclerotized intertidal mites. Interlamellar setae vestigial or minute. Lamellar ridges developed as cuticular channels or completely absent. Translamella strongly reduced or absent. Sensillus short, clavate, smooth or spinose. Tutorium absent. Van der Hammen's organ present, typical for the genus. Pedotecta present, weakly developed. Lenticulus present or absent. Notogaster with 14 pairs of setae, sometimes *c*<sub>3</sub> vestigial. Genital setae 5 pairs.

### *Fortuynia atlantica* Krisper and Schuster, 2008

#### Juveniles of *Fortuynia atlantica* – common features

Apherodermous. Colour black, cuticle shiny appears polished. Majority of integument thick sclerotized, except for lateral folds surrounding centrodorsal plate (Figure 13). Due to their dark coloration nymphs showing generally a strong similarity to adult specimens under dissecting microscope. Gastronotic region strongly dorsoventrally flattened, whole body streamlined shaped. Prodorsum triangular. Rostrum rounded demarcated from remainder of prodorsum by an inconspicuous transverse ridge. Rostral setae (*ro*) long, thin and smooth. Lamellar setae (*le*) simple, smooth, half the length of (*ro*). Exobothridial setae (*ex*) minute and interlamellar setae (*in*) only vestigial. Sensilla short, capitate and overall smooth. Bothridia cup-like, narrow orifice with lateral incision. Medially on posterior border of prodorsum two paired groups of distinct pores leading into tracheal tubes (Figure 7B); in dorsal view covered by anterior folds of gastronotic region. Gnathosoma no obvious differences to adult stage. Pedipalp pentamerous 0-2-1-3-9 (solenidion included). Rutella broad, with membranous margin. Setae *a* and *m* thin, simple of normal length. Seta *h* long, smooth and spiniform. Lateral posterior borders of mentum tip-like elongated. Hysterosoma slightly convex. Hysterosomal cupules present but difficult to trace in any stage. Large centrodorsal plate finely punctate and stronger sclerotized, bearing all notogastral setae, except for *c*<sub>1-3</sub> in all stages and seta *h*<sub>2</sub> in the



**FIGURE 8.** *A. inexpectatus*. A) larva dorsal view. B) larva ventral view. C) protonymph dorsal view. D) protonymph ventral view.



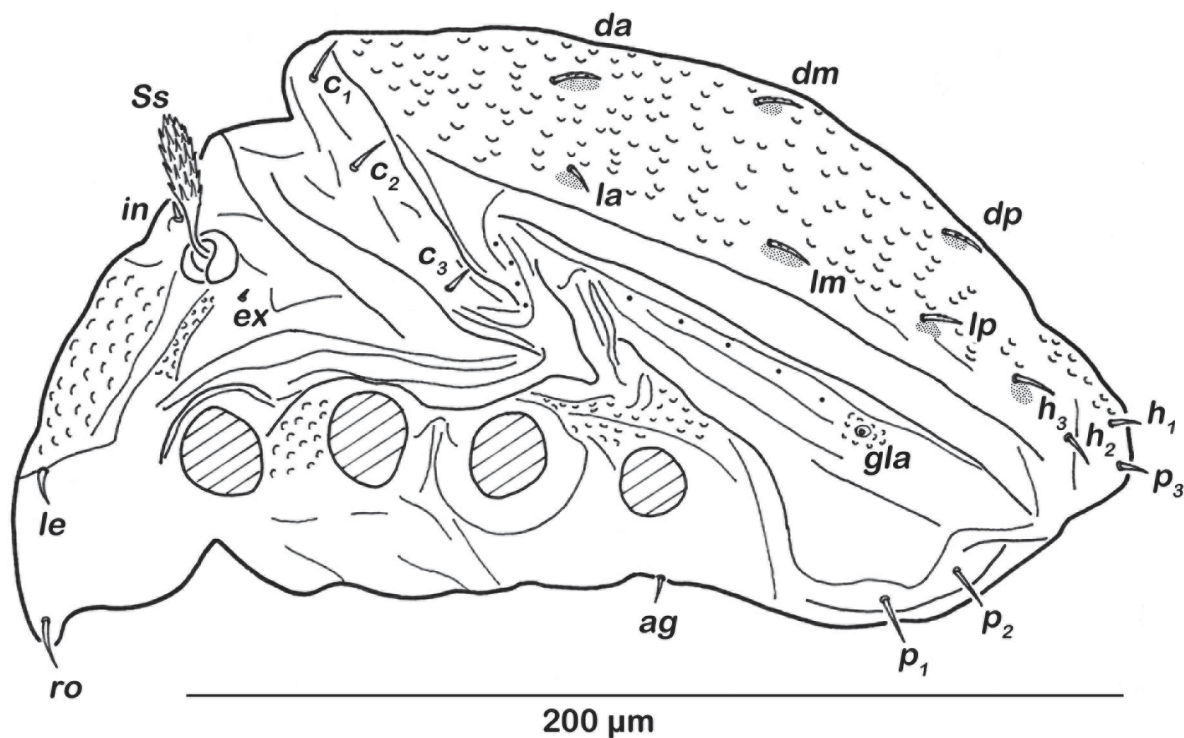


FIGURE 9. *A. inexpectatus* protonymph lateral view.

larval stage. Lateral borders of plate straight, anterior border slightly convex, posterior border strongly convex. In nymphal stages posterior part of centrodorsal plate showing a median lesser sclerotized smooth area resembling an inverted Y, whereas longitudinal line long reaching anterior third of plate. Large folds surrounding centrodorsal plate. Within lateral folds a series of longitudinally arranged fine but distinct pores, each turning into fine tracheal internal tubes (Figure 14). Orifice of opisthonotal gland (*gla*) in posterior half of lateral folds. Small porose areas associated with bases of notogastral setae. A series of large darker spots arranged in two longitudinal rows, in anterior part of centrodorsal plate spots aligned transversally connecting longitudinal rows; these darker areas generally difficult to trace. Ventrosejugal suture developed as distinct furrow, resembling medially a broad V. Nymphs with no distinct genital valves, genital orifice a longitudinal slit, inner margins with conspicuous granules. Anterior to genital opening a slightly rostrad curved canal-like fold. Posterior to anal region caudad arched furrows, along these folds singular fine pores (Figure 15). Legs monodactylous. Integument showing same pattern as in adults, trochanters dark, heavily sclerotized, proximal third of femora light, remainder dark, genua dark, tibiae light, proximal part of tarsi dark and distal parts light. Dorsal setae of tibiae and genua absent when respective solenidion present. Solenidia on tibia I inserting on small apophysis. Large porose areas on ventral paraxial side of femora I and II and on dorsal paraxial side on femora III and IV. Circular or elliptic porose areas on paraxial dorsal side of trochanters III and IV. Tarsal lyrifissure already observable in all juvenile stages.

**Larva.** Length (N=3): 226–235 μm (mean 231 μm)

Gastronotic region (Figure 16A). Eleven pairs of strong, smooth and spiniform notogastral setae; *c*<sub>1-3</sub>, *da*, *dm*, *dp*, *la*, *lm*, *lp*, *h*<sub>1-2</sub>; *h*<sub>3</sub> absent. All setae long, except for seta *dm* showing normal length, setae *c*<sub>1</sub>, *la*, *lm* and *dp* a third longer than remaining setae. Conspicuous transverse ridge on centrodorsal plate passing posterior line of setae *dm* and *lm*.

Ventral region of idiosoma (Figure 16B). Epimeral setation 3-1-2, seta *1c* shaped valve-like protecting Claparède organ. Cuticle surrounding Claparède organ anteromedially strongly sclerotized, developed as protruding protective ridge. A transverse fold anterior of anal orifice.

Legs. Setation and solenidia see table 2.

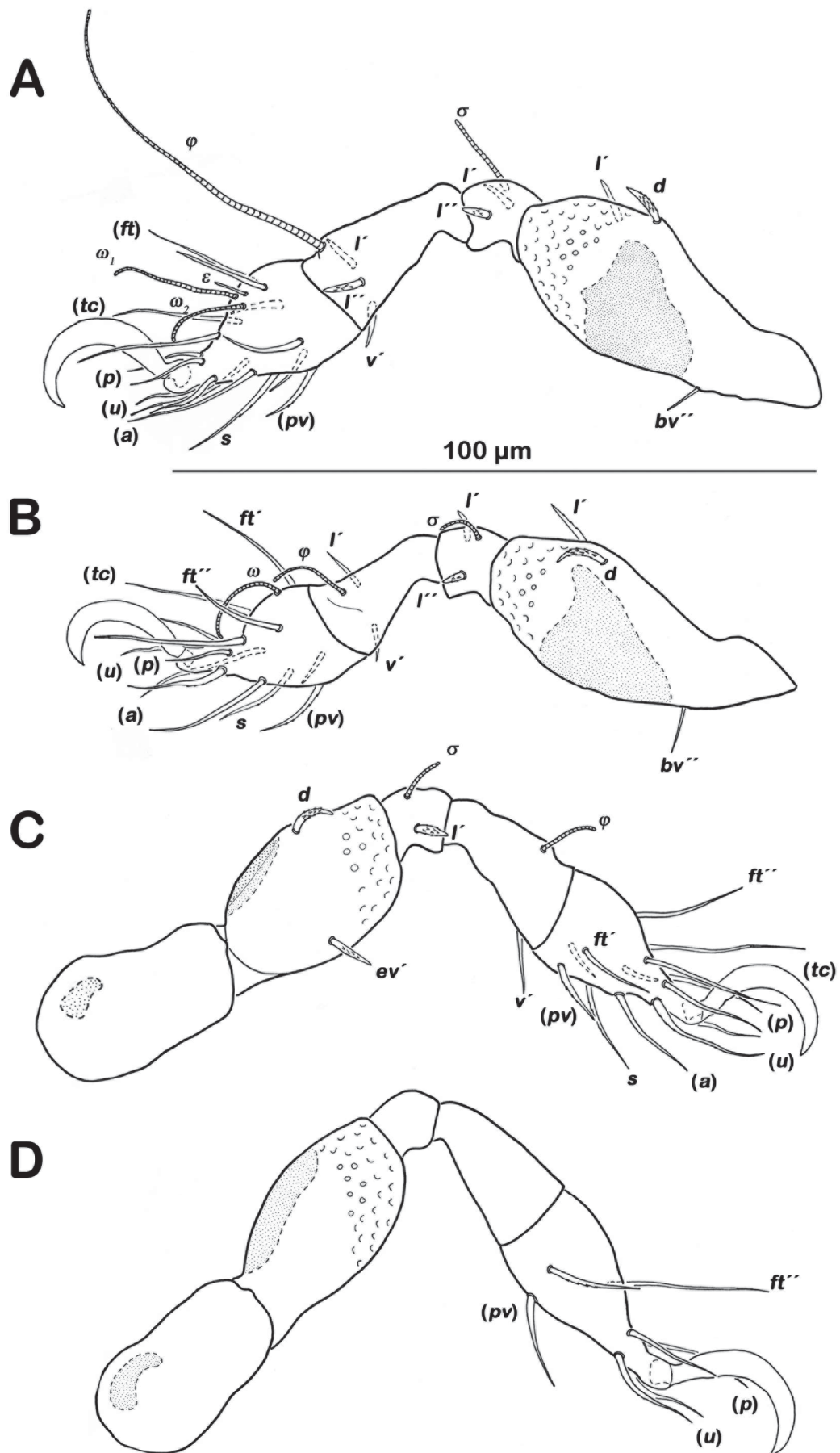
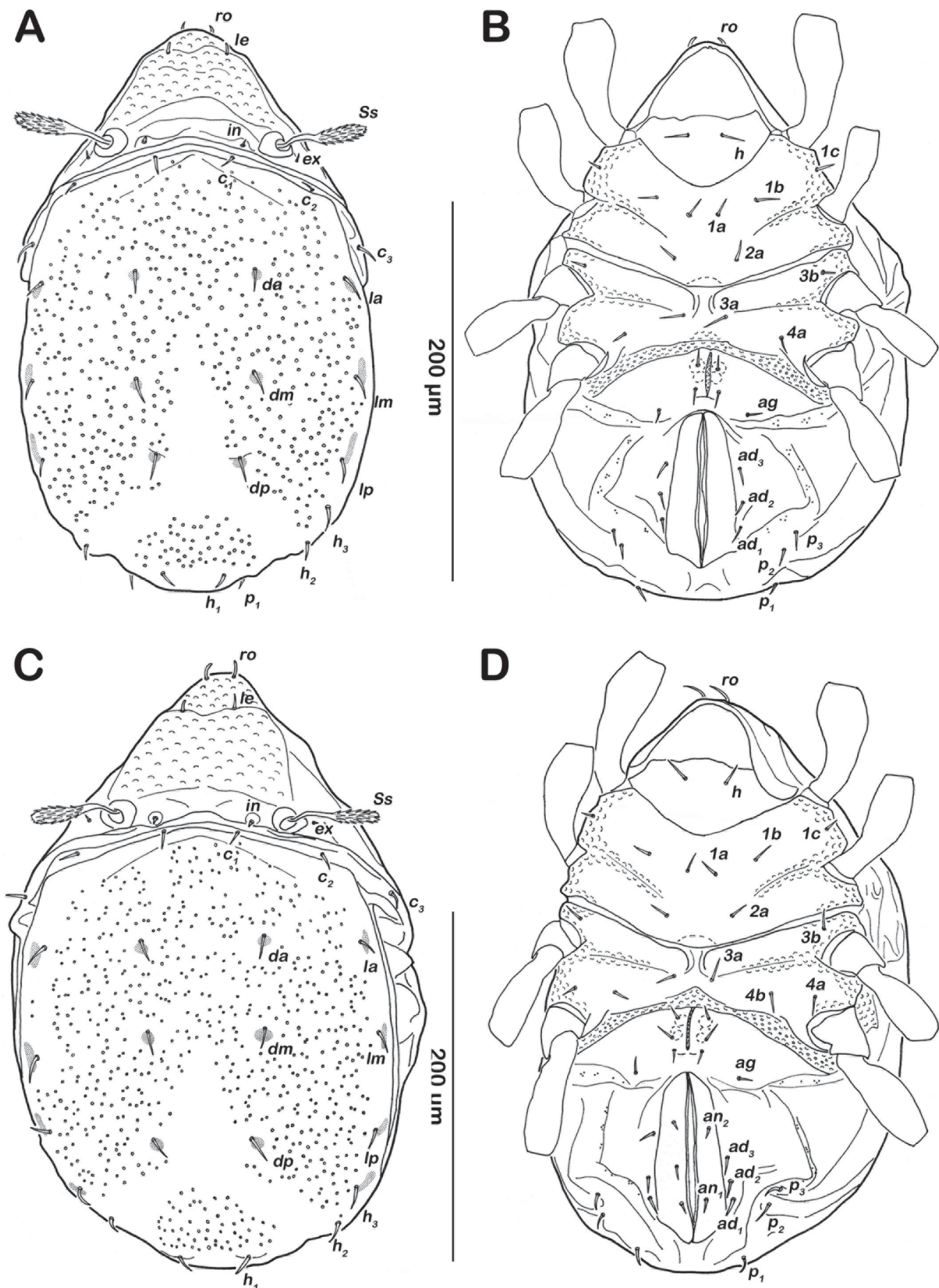


FIGURE 10. *A. inexpectatus* protonymph left legs antiaxial view. A) leg I. B) leg II. C) leg III. D) leg IV.





**FIGURE 11.** *A. inexpectatus*. A) deutonymph dorsal view. B) deutonymph ventral view. C) tritonymph dorsal view. D) tritonymph ventral view.

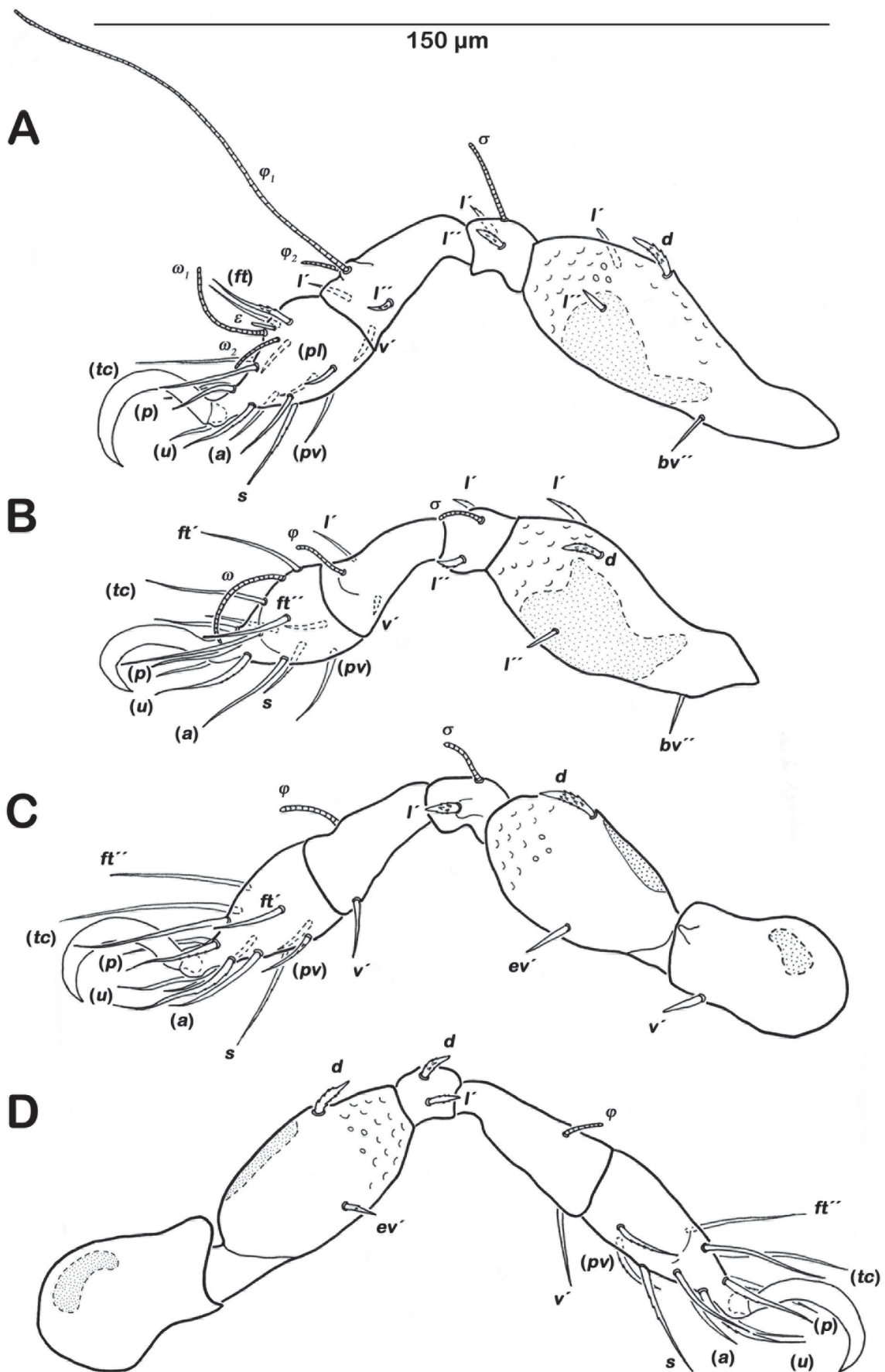
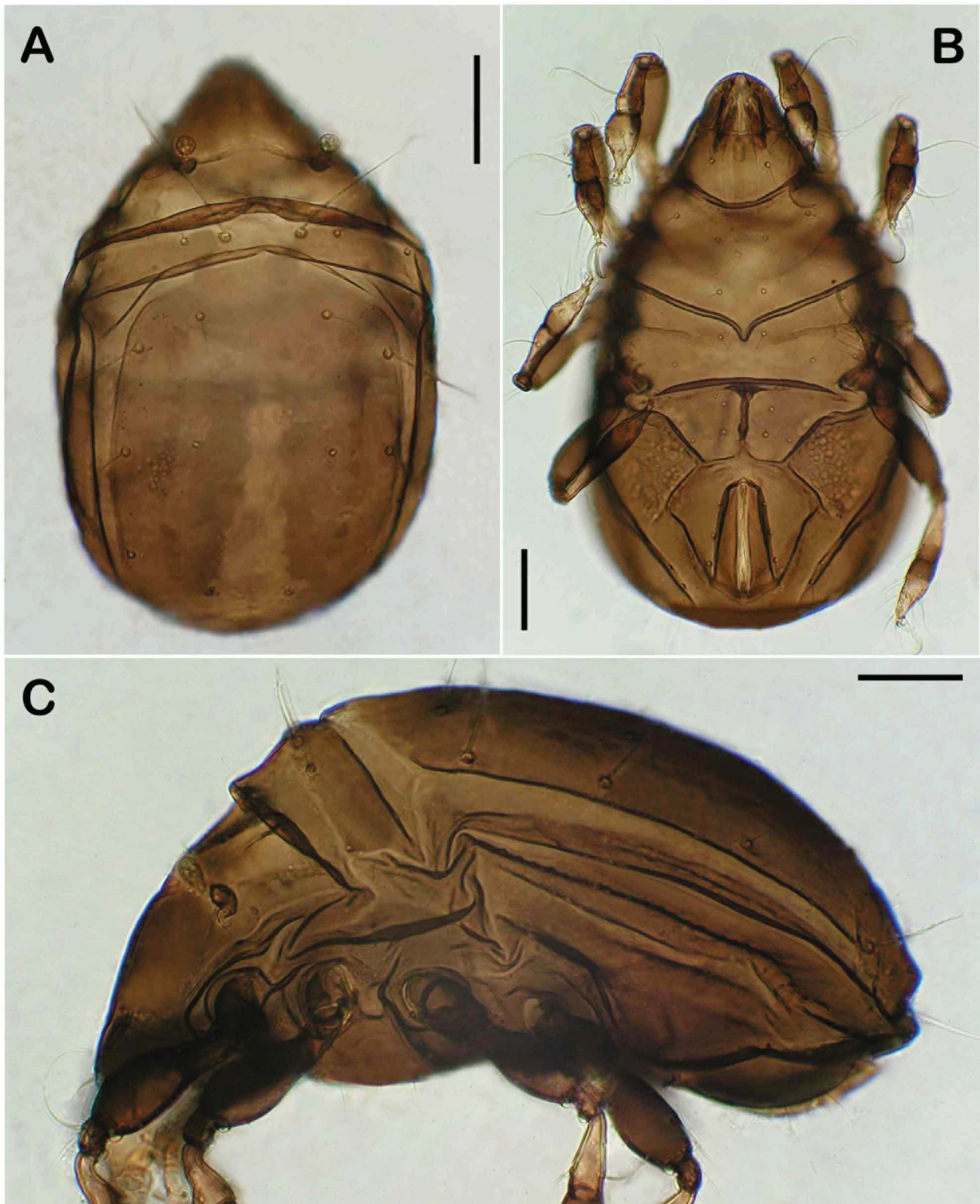


FIGURE 12. *A. inexpectatus* deutonymph legs antiaxial view. A) left leg I. B) left leg II. C) right leg III. D) left leg IV.



**FIGURE 13.** *Fortuynia atlantica* LM-micrographs. Scale bar: 50μm. A) protonymph dorsal view, layered from 13 images. B) deutonymph ventral view, layered from 10 images. C) tritonymph lateral view, layered from 10 images.

**Protonymph.** Length (N=17): 258–306 μm (mean 287 μm)

Gastronotic region (Figure 16C, 17). Fifteen pairs of notogastral setae;  $c_{1-3}$ ,  $da$ ,  $dm$ ,  $dp$ ,  $la$ ,  $lm$ ,  $lp$ ,  $h_{1-3}$  and  $p_{1-3}$ . Seta  $c_1$  and  $h_1$  longest,  $dm$ ,  $dp$  and  $h_3$  shortest. Transverse ridge on centrodorsal plate passing posterior line of setae  $dm$  and  $lm$ , absent from this stage.



Ventral region of idiosoma (Figure 16D). Epimeral setation 3-1-2-1. Seta *lc* ordinary seta, close to trochanter I, seta *4a* near trochanter IV. One pair of genital setae, located in the middle of genital area. Aggenital setae absent. Setae *p*<sub>3</sub> and *p*<sub>2</sub> flanking anal opening.

Legs (Figure 18). Chaetome and solenidia see table 2.

**TABLE 2.** *Fortuynia atlantica*. Leg setation from larva to adult. Data for adults taken from Krisper & Schuster (2008). First development of setae characterized by letters. ( ) = pairs of setae, - = no change with regard to preceding stage.

	Instars	Trochanter	Femur	Genu	Tibia	Tarsus	Chaetome	Solenidia
Leg I	larva	-	<i>d, bv''</i>	( <i>l</i> ), $\sigma$	( <i>l</i> ), <i>v'</i> , $\phi_1$	( <i>pl</i> ), ( <i>pv</i> ), <i>s</i> , ( <i>a</i> ), ( <i>u</i> ), ( <i>p</i> ), ( <i>tc</i> ), ( <i>ft</i> ), $\omega_1$	0-2-2-3-16	1-1-1
	protonymph	-	-	-	-	$\omega_2$	0-2-2-3-16	1-1-2
	deutonymph	-	<i>l'</i>	-	$j_2$	-	0-3-2-3-16	1-2-2
	tritonymph	-	<i>l''</i>	-	-	( <i>it</i> )	0-4-2-3-18	1-2-2
	adult*	<i>v''</i>	-	-	-	-	1-4-2-3-18	1-2-2
Leg II	larva	-	<i>d, bv''</i>	( <i>l</i> ), $\sigma$	<i>l'</i> , <i>v'</i> , $\phi$	( <i>pv</i> ), <i>s</i> , ( <i>a</i> ), ( <i>u</i> ), ( <i>p</i> ), ( <i>tc</i> ), ( <i>ft</i> ), $\omega$	0-2-2-2-13	1-1-1
	protonymph	-	-	-	-	-	0-2-2-2-13	1-1-1
	deutonymph	-	<i>l''</i>	-	-	-	0-3-2-2-13	1-1-1
	tritonymph	-	<i>l'</i>	-	-	( <i>it</i> )	0-4-2-2-15	1-1-1
	adult*	<i>v''</i>	-	-	<i>l''</i>	-	1-4-2-3-15	1-1-1
Leg III	larva	-	<i>d, bv'</i>	<i>l', \sigma</i>	<i>v', \phi</i>	( <i>pv</i> ), <i>s</i> , ( <i>a</i> ), ( <i>u</i> ), ( <i>p</i> ), ( <i>tc</i> ), ( <i>ft</i> )	0-2-1-1-13	1-1-0
	protonymph	-	-	-	-	-	0-2-1-1-13	1-1-0
	deutonymph	<i>v'</i>	-	-	-	-	1-2-1-1-13	1-1-0
	tritonymph	-	<i>l'</i>	-	<i>l'</i>	( <i>it</i> )	1-3-1-2-15	1-1-0
	adult*	<i>l'</i>	-	-	<i>l''</i>	-	2-3-1-3-15	1-1-0
Leg IV	protonymph	-	-	-	-	( <i>pv</i> ), ( <i>u</i> ), ( <i>p</i> ), <i>ft'</i>	0-0-0-0-7	0-0-0
	deutonymph	-	<i>d, bv'</i>	<i>d, l'</i>	<i>v', \phi</i>	<i>s</i> , ( <i>a</i> ), ( <i>tc</i> )	0-2-2-1-12	0-1-0
	tritonymph	<i>v'</i>	-	-	<i>l'</i>	-	1-2-2-2-12	0-1-0
	adult*	-	-	-	<i>l''</i>	<i>ft''</i>	1-2-2-3-13	0-1-0

**Deutonymph.** Length (N=22): 306–369  $\mu$ m (mean 341  $\mu$ m)

Gastronotic region (Figure 19A). Fifteen pairs of notogastral setae, same positions and shapes as in protonymph.

Ventral region of idiosoma (Figure 19B). Epimeral setation 3-1-2-2, seta *4b* median on epimeral plate IV. Two pairs of genital setae in a longitudinal row. One pair of simple and short aggenital setae *ag* laterad of posterior genital setae. Three pairs of adanal setae *ad*<sub>1-3</sub> flanking anal valves. Two pairs of vestiges on anal plates.

Legs (Figure 20). Chaetome and solenidia see table 2.

**Tritonymph.** Length (N=15): 395–431  $\mu$ m (mean 415  $\mu$ m)

Gastronotic region (Figure 19C). Fifteen pairs of notogastral setae, no difference to deutonymph.

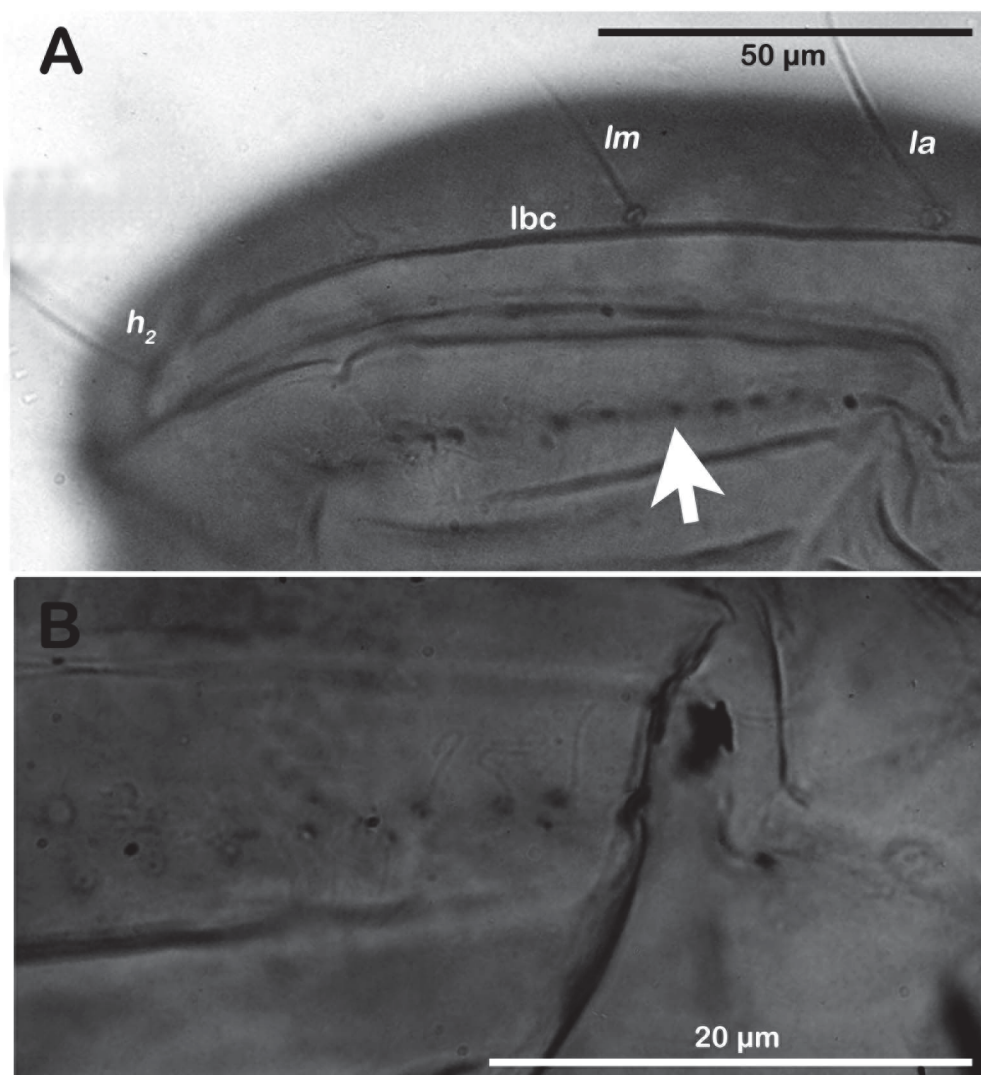
Ventral region of idiosoma (Figure 19D). Epimeral setation 3-1-3-2, seta *3c* next to trochanter III. Four pairs of short genital setae arranged in two longitudinal semicircles. One pair of aggenital setae *ag*. Three pairs of adanal setae *ad*<sub>1-3</sub> flanking anal opening, whereas *ad*<sub>1</sub> twice as long as others. Two pairs of anal setae *an*<sub>1-2</sub>.

Legs. Chaetome and solenidia see table 2.

## Discussion

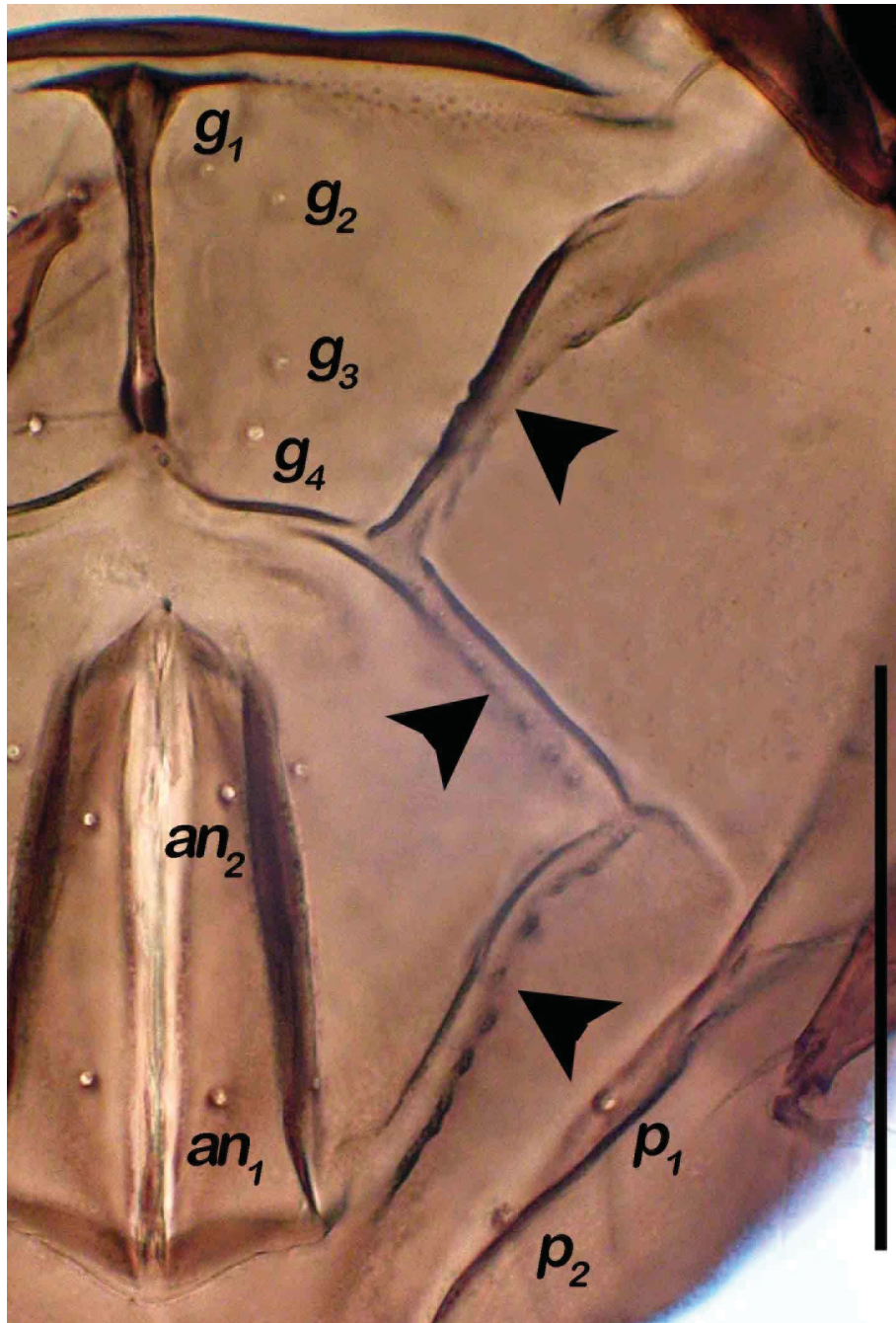
The new species *Alismobates inexpectatus* is well in accord with the diagnosis of the genus *Alismobates* given by Luxton (1992) and consequently represents a valid member of this taxon. *Alismobates inexpectatus* can be easily distinguished from the other two congeneric species due to their name-giving characters, *A. reticulatus* Luxton, 1992 showing an unique reticular notogastral pattern (Luxton 1992; Karasawa & Aoki 2005) and *A. rotundus* Luxton, 1992 exhibiting a nearly globular hysterosomal body shape (Luxton 1992). Furthermore, these species are both

of an obvious smaller size than *A. inexpectatus*, their prodorsal ridges are simple and they do not possess the conspicuous granular cuticle flanking the lenticulus. Apart from these differences, there are certain common features relating all three *Alismobates* species (table 3). Luxton (1992) already listed convergent prodorsal ridges, minute or vestigial interlamellar setae, dorsosejugal suture complete, clavate spinose sensilla, dark semicircular areas laterally of the genital field (whereas it is not clear what he meant with it), and blunt, not recurved and not expanded solenidia  $\omega_1$  on tarsi I and II as diagnostic characters for this genus. This is correct but only the combination of these features is unique to *Alismobates* within the family of Fortuyniidae. Minute or vestigial interlamellar setae and a complete dorsosejugal suture can also be found in all *Fortuynia* species (van der Hammen 1960, 1963; Luxton 1967, 1986, 1992; Aoki 1974; Marshall & Pugh 2002; Krisper & Schuster 2008; Bayartogtokh *et al.* 2009). Not recurved and not expanded solenidia  $\omega_1$  on tarsi I and II are shown in *F. marina* (van der Hammen 1960) and *F. atlantica* (Krisper & Schuster 2008) as well, and a clavate and spinose sensillus is also present in the genus *Circellobates* (Luxton 1992). Aside from Luxton's diagnostic traits, the clear demarcation of the rostrum from the prodorsum and the epimeral setation of 3-1-2-2 are common to all three *Alismobates* species, but again these characters are shared with *Circellobates* (Luxton 1992). The monotypic genus *Circellobates* differs from *Alismobates* only in the presence of two annulated pores on epimeron III, the absence of a lenticulus and recurved solenidia  $\omega_1$  on tarsi I and II (Luxton 1992). All the other shared characters indicate that both these taxa are more related to each other than to the genus *Fortuynia*.



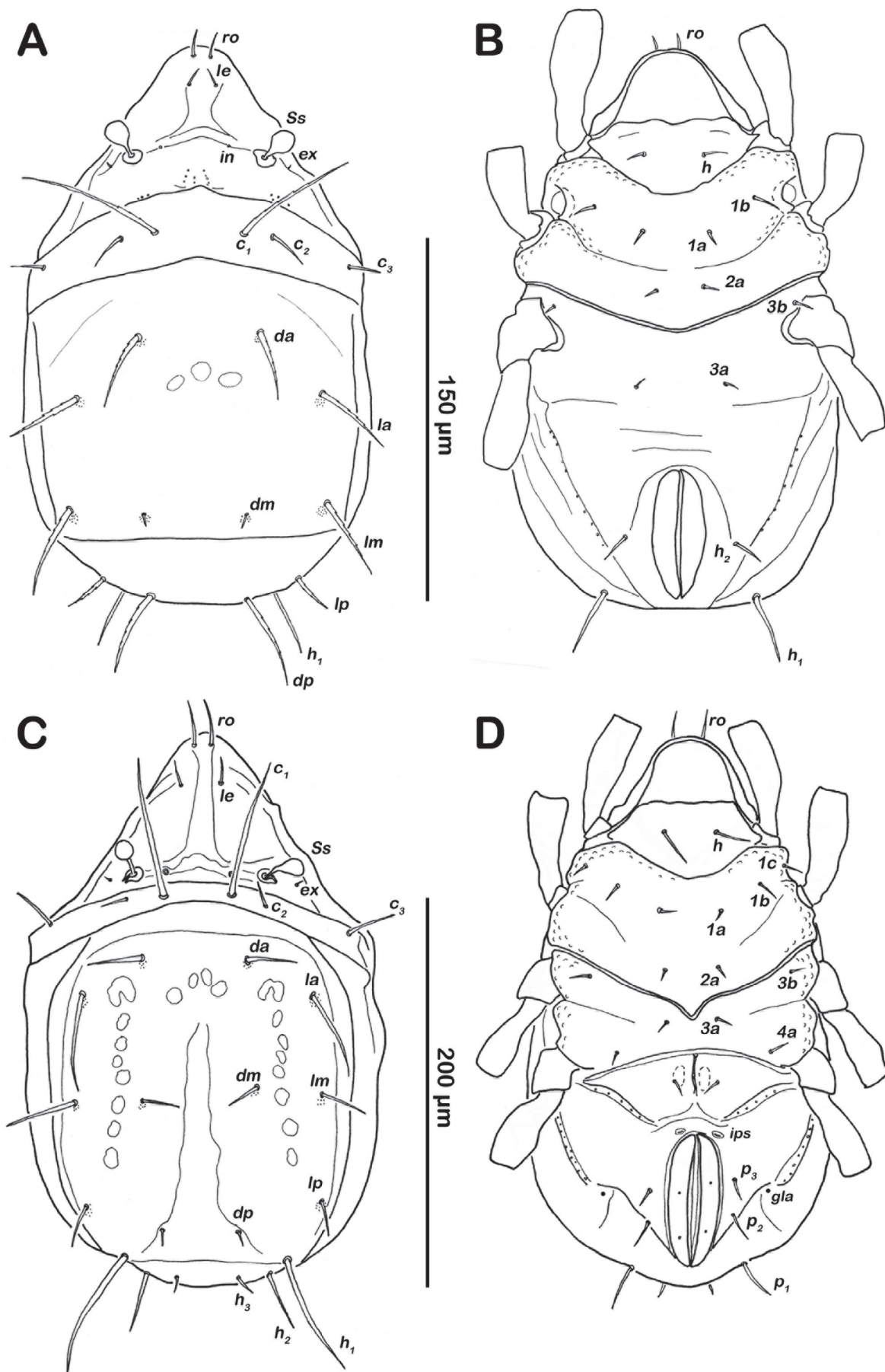
**FIGURE 14.** *F. atlantica* micrographs of nymphs, lateral view. A) lateral folds, arrow points to series of pores, lbc = lateral border of centrodorsal plate. B) enlarged view of pores associated with fine tracheal tubes (best observable in centre of photograph).





**FIGURE 15.** *F. atlantica* tritonymph, micrograph of left anogenital region. Arrowheads pointing to pores aligned in ventral furrows.

The possession of median, longitudinally arranged pairs of notogastral pores is also common to the genera *Alismobates* and *Circellobates*, whereas Luxton (1992) provided very vague descriptions of these structures, consequently a clear statement is unfeasible. In *A. reticulatus* there are four pairs of single pores, in *A. rotundus* two or three pairs are present and *C. venustus* is supposed to show several pores associated with setae, whereas at least one of which is sacculate (Luxton 1992); in the new species, *A. inexpectatus*, there are definitely four pairs of single median pores and four pores grouped semicircular on the posterior part of notogaster. Within the genus *Fortuynia*, only in *F. atlantica* the existence of three pairs of notogastral pore like-structures, with slightly different relative positions than in *Alismobates*, and up to eight such structures arranged semicircular near seta  $h_2$  were reported (Krisper & Schuster 2008). Between *A. inexpectatus* and *F. atlantica* there is a striking similarity in the arrangement of these pores, especially the ones near  $h_2$ , maybe these structures are of homologous origin. Moreover such pores may be present in more *Fortuynia* species than formerly supposed; van der Hammen (1960, 1963) was the



**FIGURE 16.** *F. atlantica*. A) larva dorsal view. B) larva ventral view C) protonymph dorsal view. D) protonymph ventral view.

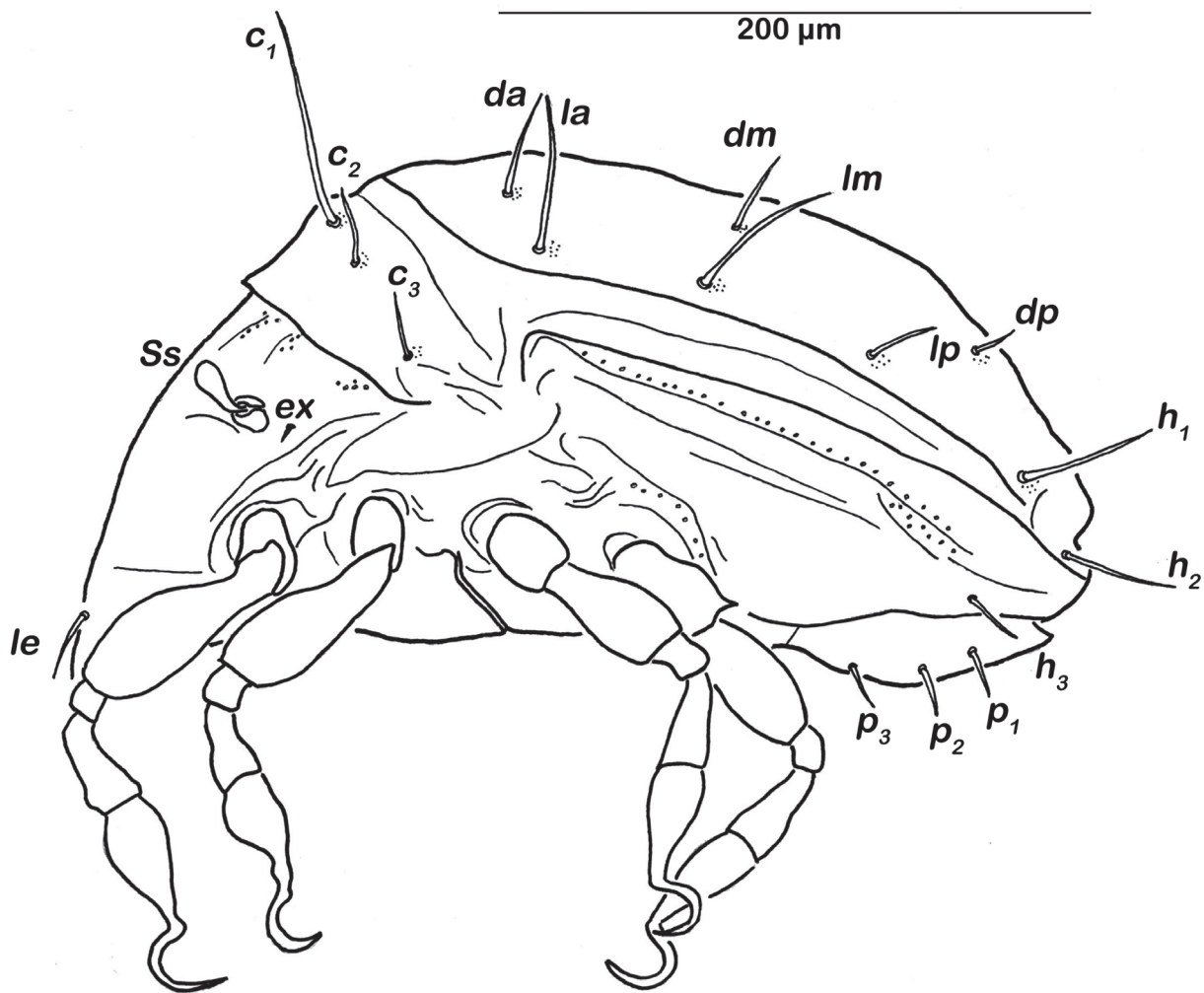
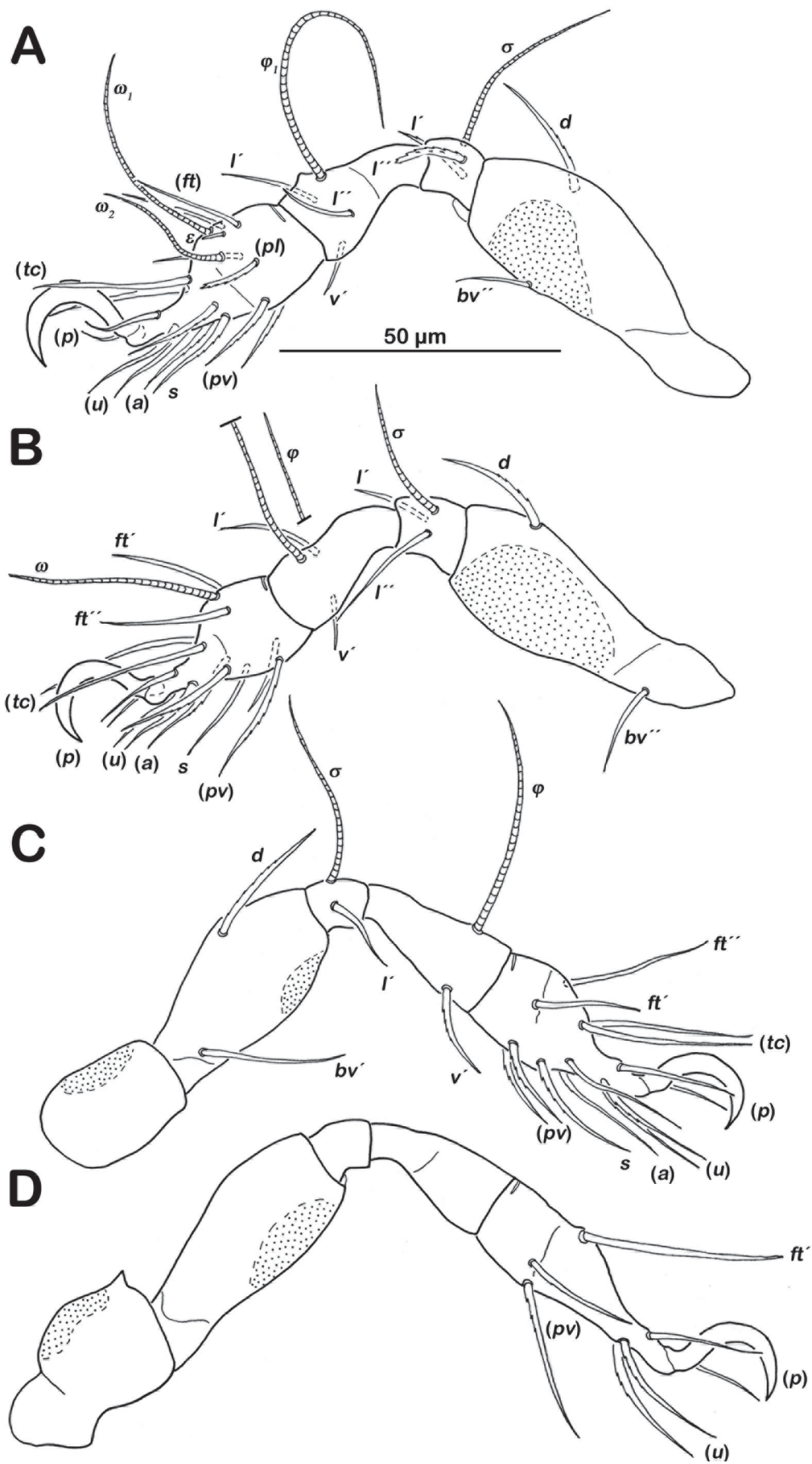


FIGURE 17. *F. atlantica* protonymph lateral view.

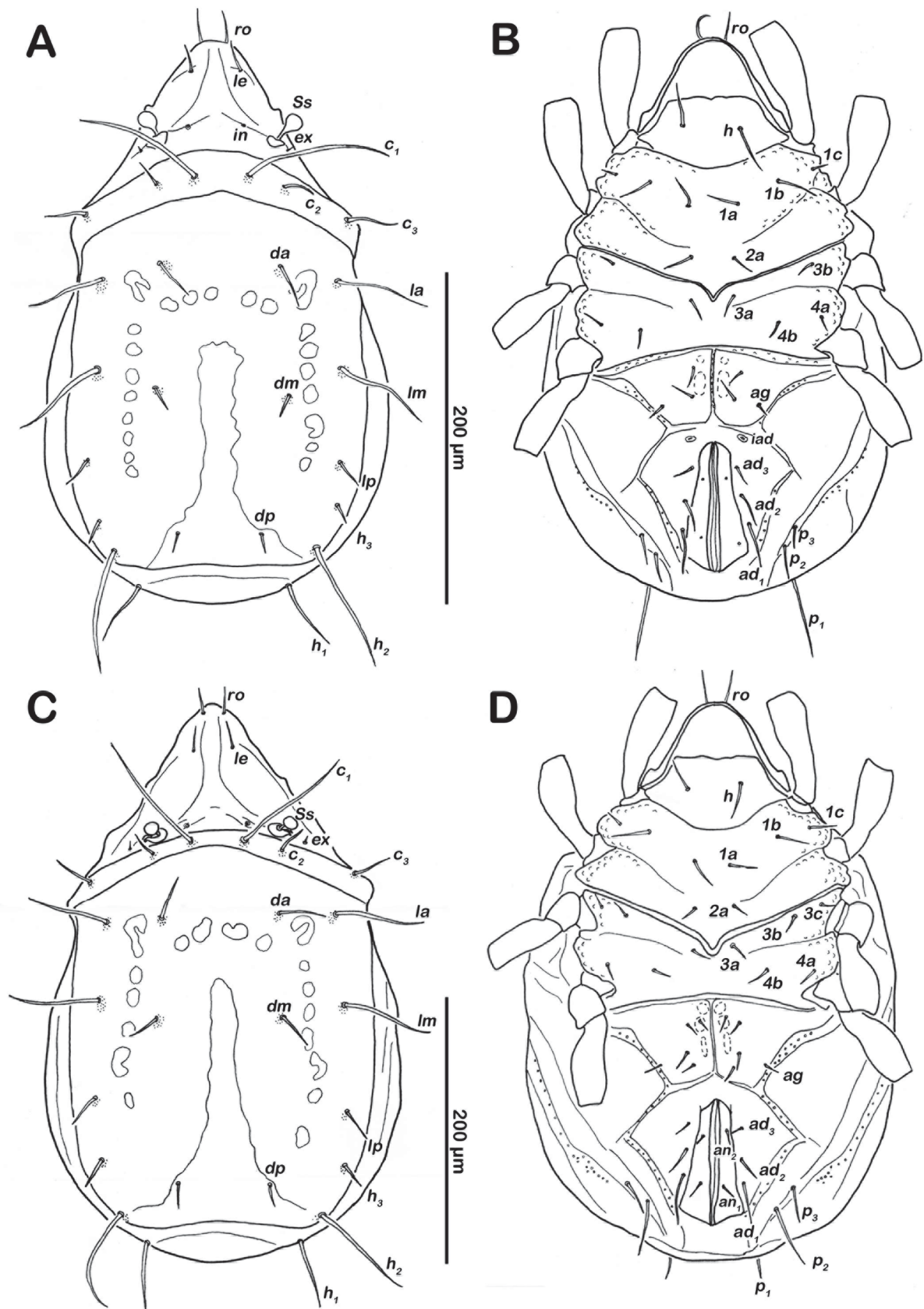
only author literally reporting the absence of porose areas on the notogaster. Luxton (1992) depicted *F. sinensis* with two pairs of pores on the gastronomic region but did not mention them in the description, nevertheless listing “minute pores associated with bases of medial setae of notogaster” as diagnostic character for the family Fortuyniidae. Further, *A. inexpectatus* also shows small porose areas associated with the bases of notogastral setae, whereas this character is already present in the juvenile stages. The porosity of these areas can also be clearly stated in the immatures of *F. atlantica*. The same may be true for the adults, but Krisper and Schuster (2008: p.422) were not absolutely sure about the porose character of these areas and wrote: “Lighter area around ring seems porose (porose area?)”. Luxton (1986: p.67-68) made a similar statement in his description of *F. maculata* writing: “Additionally in this species each setal insertion is itself associated with a lighter-coloured area of the integument”, which may also be interpreted as finely porose areas associated with the setae. All these structures are admittedly difficult to detect but may represent a morphological character of important phylogenetic and/or ecological significance. Anyway, porose rings at base of all or several notogastral setae do also exist in adults of certain *Proteremaeus* and *Eremaeus* species (Behan-Pelletier 1993) but these are without a doubt convergently evolved structures.

Another morphological trait being of great value for systematic considerations is the so-called “van der Hammen’s Organ” (Luxton 1967). This complex system of cuticular channels was supposed to be confined to the genus *Fortuynia* (van der Hammen 1963; Luxton 1967, 1986, 1990; Talker *et al.* 1981; Bayartogtokh *et al.* 2009) but the possession of this organ is indeed typical for the whole family of Fortuyniidae (Norton & Behan-Pelletier 2009). Without a doubt Luxton (1992) was aware of this circumstance and therefore classified *Alismobates* and *Circellobates*, showing this specific organ, within the family of Fortuyniidae. Luxton’s drawings clearly depict this important structure but inexplicably he did not mention the presence and the relevance of this organ in a single word.



**FIGURE 18.** *F. atlantica* protonymph left legs antiaxial view. A) leg I. B) leg II. C) leg III. D) leg IV.

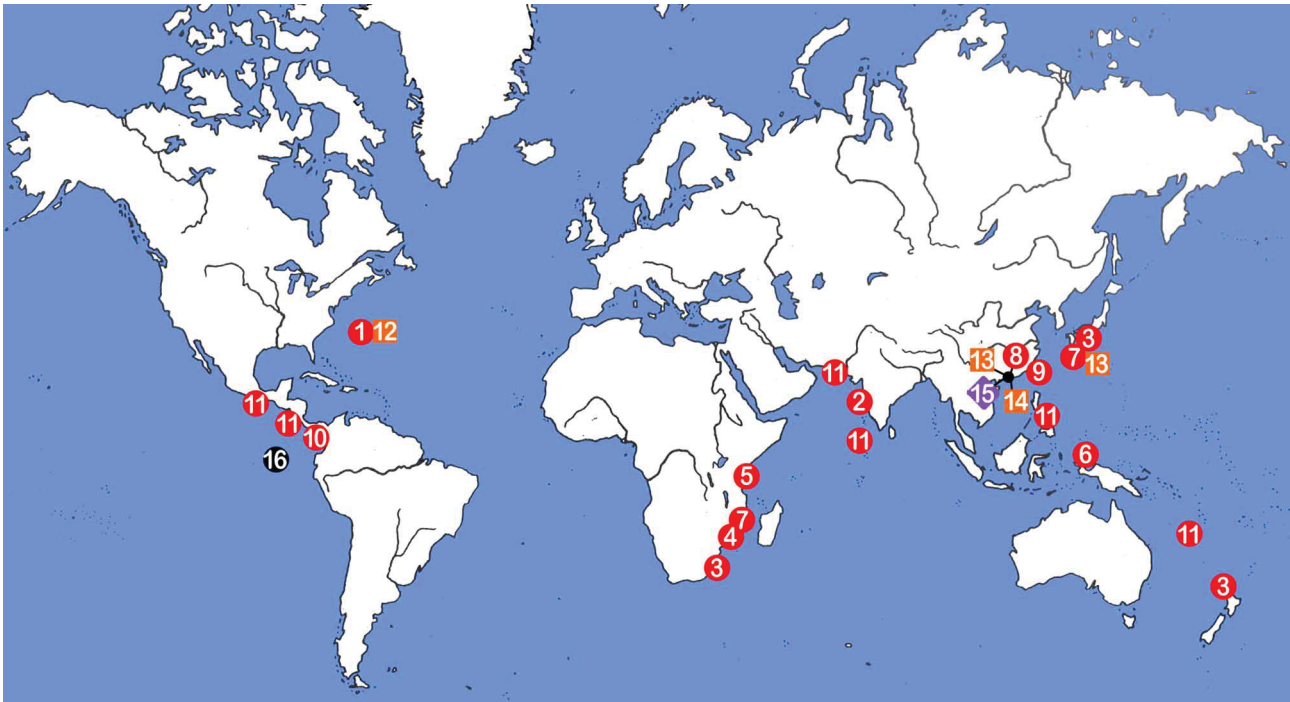




**FIGURE 19.** *F. atlantica*. A) deutonymph dorsal view. B) deutonymph ventral view. C) tritonymph dorsal view. D) tritonymph ventral view.





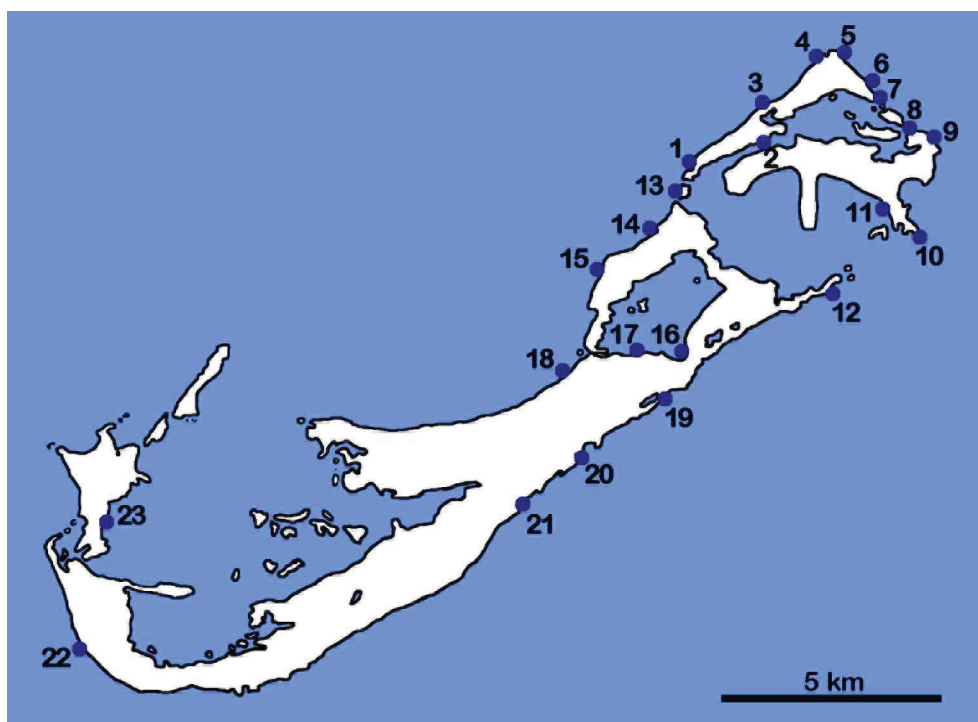


**FIGURE 21.** Geographical distribution of the family Fortuyniidae. Circles = *Fortuynia*, squares = *Alismobates*, trapezoid = *Circellobates*, black circle = Fortuyniidae gen. sp.

1. *F. atlantica*: Bermuda (Krisper & Schuster 2008); 2. *F. arabica*: India (Bayartogtokh *et al.* 2009); 3. *F. elamellata*: New Zealand (Luxton 1967), Japan (Aoki 1974), South Africa (Marshall & Pugh 2002); 4. *F. inhambanensis*: Mozambique (Marshall & Pugh 2002); 5. *F. maculata*: Kenya (Luxton 1986); 6. *F. marina*: New Guinea (van der Hammen 1960); 7. *F. rotunda*: Mozambique (Marshall & Pugh 2002), Japan (Karasawa & Aoki 2005); 8. *F. sinensis*: Hong Kong (Luxton 1992); 9. *F. taiwanica*: Taiwan (Bayartogtokh *et al.* 2009); 10. *F. yunker*: Panama (van der Hammen 1963); 11. *Fortuynia* sp.: Philippines (Talker *et al.* 1981), Costa Rica, Pakistan, New Caledonia, Mexico, Maldives (Schuster 1989), Mauritius (Schuster 1998, unpublished); 12. *A. inexpectatus*: Bermuda; 13. *A. reticulatus*: Hong Kong (Luxton 1992), Japan (Karasawa & Hijii 2004, Karasawa & Aoki 2005); 14. *A. rotundus*: Hong Kong (Luxton 1992); 15. *C. venustus*: Hong Kong (Luxton 1992); 16. Fortuyniidae gen. sp.: Galápagos (Schatz 1998).

However, the present study demonstrates the presence of a “van der Hammen’s Organ” in the new species *A. inexpectatus*, whereas there are some conspicuous divergences from the *Fortuynia* typical scheme (Figure 3B). *Fortuynia* basically shows a prodorsal anterior canal (*ce*) passing ventrally of the bothridium, a main lateral channel running from the dorsosejugal furrow to the ventrosejugal furrow, a short posterior canal leading to acetabulum III and a further posterior channel reaching acetabulum IV (van der Hammen 1963; Luxton 1967; Pugh *et al.* 1990; Marshall & Pugh 2002; Krisper & Schuster 2008); in *F. maculata* there is an additional anterior granular groove leading above acetabulum II to acetabulum I (Pugh *et al.* 1990, p. 1533 “k” on Fig. 3). In *A. inexpectatus*, on the other hand, the anterior dorsal furrow (*ce*) is lacking and instead there is a short channel connecting the main lateral canal with the bothridium, further the posterior parts running to acetabulum III and IV are less complex, meaning more opened and groove-like and anteriorly there is a distinct channel leading ventrally to acetabulum I, this channel is absent in *Fortuynia*. Expressed in simplified terms, in *Fortuynia* the anterior ventral parts of the “van der Hammen’s Organ” are less developed or less complex than the posterior ones and in *A. inexpectatus* the opposite is realized (see Figure 3). According to Luxton’s ventral depictions of *A. reticulatus* and *A. rotundus* (Luxton 1992), the anterior channel running ventrad of pedotectum I to acetabulum I is present in both of these species. But the redescription of *A. reticulatus* provided by Karasawa and Aoki (2005) differs in this aspect, lacking the structure completely. The lateral depiction of *Circellobates* (Luxton 1992) exhibits a system of channels obviously representing the “van der Hammen’s Organ” but the drawings are not detailed enough to reveal the distinct nature of this system. Due to this inconsistency and incomplete information it is not possible to determine if the presence of an anterior ventral channel is specific for the genus *Alismobates*. Nevertheless, the “van der Hammen’s Organ” is implicated in gas exchange and pressure equalization during tidal inundation (Pugh *et al.* 1990), correspondingly its function is vital to survive in the intertidal environment. Thus this organ may be

subject to strong selective constraints and therefore its particular formation in different taxa may play a major role in future systematic and phylogenetic considerations.



**FIGURE 22.** Distribution of *Alismobates inexpectatus* on the archipelago of Bermuda. (Collected by T. Pfingstl 2011 and R. Schuster 1977 and 1981)

1. Whalebone Bay, 2. Concrete Beach, 3. Rocky Hill Park, 4. Tobacco Bay, 5. Gates Bay, 6. Building Bay, 7. Town Cut, 8. Gunner Bay, 9. Fort Popple, 10. Gurnet Head, 11. Cooper's Island, 12. Howard Bay, 13. Coney Island, 14. Bailey's Bay, 15. Crawl Hill, 16. Devil's Hole, 17. Harrington Sound, 18. Penhurst Park, 19. Spittal Pond, 20. Devonshire Bay, 21. Hungry Bay, 22. Whitney Bay, 23. Scaur Hill Park.

Locations divided into respective Parishes: 1–12 St. George's, 13–15 Hamilton, 16–19 Smith's, 20 Devonshire, 21 Paget, 22 Southampton and 23 Sandy's.

Similarly, only a provisional and incomplete comparison of leg features of *Alismobates* and *Circellobates* can be given, as neither Luxton (1992) nor Karasawa and Aoki (2005) provided extensive information on these morphological characters. Luxton (1992) observed in *A. reticulatus* and *A. rotundus* two solenidia on tibia II, but *A. inexpectatus* bears only one solenidia on the respective segment. *Alismobates reticulatus* (Luxton 1992) shows a dorsal tooth on each claw, such a tooth is lacking in *A. inexpectatus* and *A. rotundus* (Luxton 1992). Interestingly Karasawa and Aoki (2005) also reported the absence of this tooth in their redescription of *A. reticulatus*, but this difference may be added to other found variations, e.g. relative positions of certain setae, representing divergences of minor significance between the populations from Hong Kong and the Ryukyu Islands. *Alismobates inexpectatus* exhibits large porose areas on femur I to IV and smaller ones on trochanters III and IV. In *A. reticulatus* (Luxton 1992; Karasawa & Aoki 2005), *A. rotundus* and in *C. venustus* (Luxton 1992) the presence of such structures was not reported, but the possession of porose areas on certain leg segments is a widespread phenomenon among species dwelling in very moist habitats or environments subject to periodic inundation (Norton *et al.* 1997). Within the Fortuyniidae porose areas on the legs are also known to occur in *F. atlantica* (Krisper & Schuster 2008), *F. arabica*, *F. taiwanica* (Bayartogtokh *et al.* 2009), *F. elamellata* (Luxton 1967), *F. elamellata shibai* (Aoki 1974), *F. marina* (van der Hammen 1960) and *F. yunkerii* (van der Hammen 1963), whereas in *A. inexpectatus*, *F. atlantica*, *F. arabica* and *F. taiwanica* (Bayartogtokh *et al.* 2009) these areas are already present in the juvenile stages. In the other *Fortuynia* species information on the legs is simply missing, therefore it is assumable that these organs do exist in the whole genus and the family Fortuyniidae respectively.

Data on the larva and nymphs of Fortuyniidae are also generally scarce and mostly incomplete. Aside from the present description of *F. atlantica* juveniles, information exists only on the immatures of *F. yunkerii* (van der Hammen 1963), *F. elamellata* (Luxton 1967), *F. arabica* and *F. taiwanica* (Bayartogtokh *et al.* 2009) (table 4). The

juveniles of *A. inexpectatus*, described in this paper, are yet the only known immatures of the genus *Alismobates*, and though Luxton (1992) provided a dorsal and ventral depiction of a *Circellobates* tritonymph, his drawings are too sketchy and not detailed enough to allow comparison. Only the presence of a smooth notogastral plate in *Circellobates* nymphs can be stated with certainty. However, the present study demonstrates the presence of an inverted Y-shaped structure on the posterior part of this centrodorsal shield in *A. inexpectatus* and *F. atlantica* juveniles. Interestingly, in other fortuyniidae immatures this structure has not been reported (van der Hammen 1963; Luxton 1967; Bayartogtokh *et al.* 2009). Small circular porose areas associated with the bases of notogastral setae, as well as pores located in the lateral gastronomic folds are again only shown by *A. inexpectatus* and *F. atlantica*, whereas these structures may be easily overlooked, especially the pores hidden in the folds. The prodorsal pores and the pores within the lateral folds are part of a complex plastron system, which is used to breathe while being submerged (own observations; the details of this plastron system are beyond the scope of the present publication but will be described in a separate paper). Accordingly one can assume that these characters, fulfilling an important respiratory function, are at least shared among further immatures of Fortuyniidae. Although the pores located posteromedially on the prodorsum show the same position as the porose areas in immatures of for example *Tegeocranellus* (Behan-Pelletier 1997), *Cymbaeremaeus cymba* (Pfingstl & Krisper 2011a), *Micreremus brevipes* (Pfingstl & Krisper 2011b) or *Unduloribates undulatus* (Pfingstl & Krisper 2010) a homologous origin of these two structures should not be assumed for the first. The prodorsal pores of the juveniles of *A. inexpectatus* and *F. atlantica* are associated with fine tracheal tubes and fulfil, as already stated, a respiratory function whereas it is not clear if the prodorsal areas of the above mentioned taxa are organs of respiration or secretion.

In the larva of *F. yunkeri* (van der Hammen 1963) seta  $h_3$  is reduced to a vestige, whereas it is completely absent in the larvae of *A. inexpectatus* and *F. atlantica*. The same gastronomic setal deficiency is shown in Tegeocranellidae and Selenoribatidae and therefore assumed a synapomorphy for these families (Behan-Pelletier 1997). Nymphs of Fortuyniidae are generally unideficient but the juveniles of *F. arabica* and *F. taiwanica* (Bayartogtokh *et al.* 2009) differ oddly in this aspect. The protonymph of *F. taiwanica* possesses 15 pairs of notogastral setae, whereas the deutonymph exhibits only 14 pairs, losing  $p_3$ . In the deutonymph of *F. arabica* there are only 10 pairs of notogastral setae, with  $c_1$ ,  $c_2$ ,  $c_3$ ,  $da$  and  $dp$  reduced, but the tritonymph shows again 15 pairs. Such variations during the ontogeny are very unusual because typically the number of notogastral seta is constant during nymphal development, at least the reappearance of a lost seta in a following stage is exceptional. But the juveniles of *F. arabica* show more startling changes during ontogeny. The notogastral setae of the deutonymph are conspicuously different in their lengths, whereas these setae are sized all the same in the tritonymph. Moreover the deutonymph exhibits distinct genital sclerites but the tritonymph is lacking these. A detailed investigation of all developmental stages of *F. arabica* would be necessary to elucidate the reasons for these uncommon ontogenetic variations. Nevertheless, the comparison of all known immatures of Fortuyniidae clearly shows that the majority of juvenile morphological features of *Alismobates inexpectatus* conforms with that of *Fortuynia*. Thus the ontogenetic aspect also justifies the position of *Alismobates* within the family of Fortuyniidae.

The smooth centrodorsal notogastral plate framed by large folds shown in juveniles of the Fortuyniidae (van der Hammen 1963; Luxton 1992) is also common in the Selenoribatidae (Grandjean 1966, 1968; Schuster 1963) and Tegeocranellidae (Behan-Pelletier 1997) and therefore considered to be a synapomorphy of these families (Behan-Pelletier 1997). We agree with the latter author that the special nature of the plicate integument is unique among oribatids with wrinkled nymphs, e.g. *Cymbaeremaeoidea*, *Licneremaeoidea*, *Tectocephoeoidea* (Grandjean 1954), indicating a common ancestry of Fortuyniidae, Selenoribatidae and Tegeocranellidae. Whereas the details of this specific pattern may be distinct for each single family, in Tegeocranellidae and Fortuyniidae, for instance, the centrodorsal plate is slightly convex and large covering nearly the whole gastronomic region in dorsal view (van der Hammen 1963; Luxton 1967; Behan-Pelletier 1997; Bayartogtokh *et al.* 2009) but in Selenoribatidae it is hardly convex, smaller, overcasting only about two thirds of this area (Schuster 1963; Grandjean 1966, 1968; own observations). The ventrosejugal furrow of Fortuyniidae is a conspicuous and continuous medially slightly V-shaped groove and there is a further obvious transversal furrow passing the anterior border of the genital area (van der Hammen 1963; Bayartogtokh *et al.* 2009), in Selenoribatidae the ventral sejugal furrow is similarly but less distinct shaped and the latter furrow is absent (Grandjean 1966, 1968; own observations), whereas in Tegeocranellidae the ventrosejugal furrow is medially interrupted and the transverse groove anterior of the genital orifice is lacking (Behan-Pelletier 1997).



**TABLE 3.** Comparison of selected characteristics of fortunyniid species. For reasons of simplicity all *Fortunynia* species are subsumed under “*Fortunynia*”; most frequent character states are marked bold; ? = no information available in literature.

	<i>Alismobates inexpectatus</i>	<i>Alismobates reticulatus</i>	<i>Alismobates rotundus</i>	<i>Circellobates venustus</i>	<i>Fortunynia</i>
body length	347-391 µm	290-315 µm	310-320 µm	277-302 µm	409-598 µm
body width	235-253 µm	190-215 µm	230-260 µm	140-158 µm	206-468 µm
translamella	demarcating rostrum	demarcating rostrum	demarcating rostrum	demarcating rostrum	<b>absent</b> / faint ridge
exobothridial setae	minute	?	?	?	<b>vestigial</b> / minute
interlamellar setae	minute	minute or vestigial	minute	short	<b>vestigial</b> / minute
prodorsal ridges	large, thickened cuticle	small, converging	small, converging	-	<b>channels</b> / -
sensillus	clavate, spinose	clavate, spinose	clavate, spinose	clavate, spinose	clavate, <b>smooth</b> / spinose
tutorium	+	+	+	+	-
pedipalp	0-2-1-3-9	?	?	?	0-2-1-3-9
solenidion on palp	not associated, not on apophysis	?	?	?	not associated, not on apophysis
v.d. Hammen's Organ	+	+	+	+	+
pedotecta	+	+	+	+	+
surface notogaster	granular	densely punctate, reticular	finely punctate	finely punctate	<b>finely punctate</b> / granular
lenticulus	+	+	+	-	+ / -
notogastral setation	14	14	14	14	<b>14</b> / <i>c</i> <sub>3</sub> vestigial
porose areas notogaster	associated with setae	-	-	-	- / +
pores on notogaster	4 pairs + group of 4 near <i>h</i> <sub>2</sub>	4 pairs tiny pores	2-3 pairs dot pores	pores, sacculi	<b>absent</b> / 4 pairs + group of 4 near <i>h</i> <sub>2</sub>
epimeral setation	3-1-2-2	3-1-2-2	3-1-2-2	3-1-2-2	<b>3-1-3-2</b> / 3-1-3-3 / 3-1-2-3
g	4	4	4	4	5
ag	1	1	1	1	<b>1</b> / -
ad	3	3	3	3	<b>3</b> / 2
an	2	2	2	2	2
iad	posterior near <i>ad</i> <sub>2</sub>	posterior near <i>ad</i> <sub>2</sub>	posterior near <i>ad</i> <sub>2</sub>	posterior near <i>ad</i> <sub>2</sub>	posterior near <i>ad</i> <sub>2</sub>
legs	monodactylous	monodactylous (dorsal tooth)	monodactylous	monodactylous	monodactylous
legs cuticle	non-uniformly sclerotized	?	?	?	non-uniformly sclerotized
legs porose areas	+	?	?	?	+
sexual dimorphism	-	-	-	-	- / +

**TABLE 4.** Summary of character state distribution in yet known immatures of the Fortuyniidae. fe = femur, tro = trochanter; ? = no information available.

	<i>A. inexpectatus</i>	<i>F. atlantica</i>	<i>F. arabica</i>	<i>F. elamellata</i>	<i>F. taiwanica</i>	<i>F. yunkeri</i>
plication type	dorsal plate, folds	dorsal plate, folds	dorsal plate, folds	dorsal plate, folds	dorsal plate, folds	dorsal plate, folds
centrodorsal plate	foveate	finely punctate	smooth	punctate	smooth	smooth
interlamellar setae	minute	vestigial	minute	vestigial	vestigial	vestigial
exobothridial setae	minute	vestigial	minute	vestigial	vestigial	-
setation notogaster La-Ny	11-15	11-15	?-10/15	?-15	?-15/14	11-15
porose areas at bases setae	+	+	-	-	-	-
pores in folds	+	+	?	?	?	?
inverted Y on centrodorsal plate	+	+	-	-	-	-
dark spots on centrodorsal plate	+	+	-	-	+	-
epimeral setation larva	3-1-2	3-1-2	?	2-1-2	?	2-1-2
protonymph	3-1-2-1	3-1-2-1	?	3-1-2-1	3-1-2-1	3-1-2-1
deutonymph	3-1-2-1	3-1-2-2	3-1-2-2	3-1-2-2	3-1-2-2	3-1-2-2
tritonymph	3-1-2-2	3-1-3-2	3-1-3-3	3-1-3-2	?	3-1-3-2
genital setal ontogeny PN-TN	1-2-3	1-2-4	?-3-4	1-2-4	1-3-?	1-2-4
aggenital setal ontogeny PN-TN	0-1-1	0-1-1	?-0-1	0-1-1	0-0-?	0-1-1
adanal setal ontogeny PN-TN	0-3-3	0-3-3	?-3-3	0-3-3	1-3-?	0-3-3
anal setal ontogeny DN-TN	0-2	0-2	2-2	0-2	0-?	0-2
genital sclerites	-	-	+	-	-	-
ventrosetal furrow	continuous	continuous	continuous	?	continuous	continuous
furrow anterior genital orifice	conspicuous	conspicuous	conspicuous	conspicuous	conspicuous	conspicuous
porose areas fe I-IV, tro III-IV	+	+	+	?	+	?

**TABLE 5.** Comparison of certain adult and juvenile characters of the members of Ameronothroidea. This table represents a modified version of the table provided by Behan-Pelletier (1997, Table 1, p.542), whereas only updated character states are listed for the families of Ameronothroidea exclusively.

	Fortuyniidae	Selenoribatidae	Tegeocranellidae	Ameronothridae
lifestyle	intertidal	intertidal	semiaquatic	intertidal-terrestrial
Adults				
tutorium	+/-	-	+	-
dorsosejugal suture	complete	complete/incomplete	complete	complete/incomplete
lenticulus	+/-	-	+	-
notogastral setae	14	13-15	10-12	14-15
epimeral setation	3-1-2-2	1-0-1-1	2-1-2-3	3-1-2-2
or	3-1-2-3			3-1-2-3
or	3-1-3-2			
or	3-1-3-3			
genital setal ontogeny	1-2-3-4	1-2-3-3	1-3-5-6	1-3-5-6
PN-AD	1-2-4-5			
setae $\psi_2$ of ovipositor	0	1	1	2
genital-anal orifice	closely adjacent	closely adjacent	closely adjacent	distant
solenidion $\omega_2$ on tarsus II	+/-	-	-	+/-
legs porose areas	+	+	+	-/brachytrachea
tarsi	monodactylous	monodactylous	monodactylous	mono-/tridactylous
Juveniles				
centrodorsal plate	large	medium	large	-
larval seta $h_3$	-/vestigial	-	-	+
ventrosejugal suture	continuous	continuous	medially interrupted	medially interrupted
furrow anterior genital orifice	conspicuous	-	-	-

In summary, the genus *Alismobates* shares most of its characters with the genus *Circellobates*, indicating a very close relationship of these two groups. Only the presence of two conspicuous annulated pores on epimeron III and the absence of a lenticulus clearly separate *Circellobates* from *Alismobates*. The orientation of the solenidia on tarsus I and II, mentioned by Luxton (1992) also as distinguishing character, may be a preparation artefact and therefore should be used with caution. The genus *Fortuynia* is separated unambiguously from the above mentioned genera by showing a third seta on epimeron III and/or epimeron IV respectively, the possession of five pairs of genital setae and the absence of a conspicuous translamellar ridge clearly demarcating the rostrum from remainder of prodorsum (van der Hammen 1960, 1963; Luxton 1967, 1986, 1992; Aoki 1974; Marshall & Pugh 2002; Krisper & Schuster 2008; Bayartogtokh *et al.* 2009). The majority of the other yet known characters do either vary within the genus *Fortuynia* or are shared with *Alismobates* and *Circellobates*. Other morphological traits with possible systematic significance, such as the configuration of the “van der Hammen’s Organ”, notogastral pores, porose areas associated with notogastral setae or certain features of the legs must be excluded from present considerations as the knowledge about the real distribution of these characteristics is by far incomplete or at least uncertain. But future studies on fortuyniid mites should pay attention to the existence and specific arrangement of above-mentioned characters.

The creation of a new key of fortuyniid species is beyond the scope of this paper, as several authors provided subsequently keys for fortuyniid species (Luxton 1986, 1992; Marshall & Pugh 2002; Bayartogtokh *et al.* 2009), most of them still valid and correct. Nevertheless, van der Hammen (1963) and Luxton (1992) as well as Behan-Pelletier (1997, Table. 1, 542p) provided diagnostic characters for the family Fortuyniidae but recent descriptions of further new fortuyniid species (Marshall & Pugh 2002; Krisper & Schuster 2008; Bayartogtokh *et al.* 2009), as well as the present study, necessitate an update and revision of these diagnoses (table. 5). Van der Hammen (1963) and Behan-Pelletier (1997) listed a genital setal ontogeny of 1-2-4-5 as typical for the Fortuyniidae, but *F. arabica* and *F. taiwanica* (Bayartogtokh *et al.* 2009) diverge in certain nymphal stages from this scheme and *A. inexpectatus* shows a distinct different developmental pattern of 1-2-3-4. An epimeral setation of 3-1-3-2 was also supposed to be common to Fortuyniidae (van der Hammen 1963; Behan-Pelletier 1997) whereas Luxton (1992) listed 3-1-2-2 as diagnostic. But again *F. arabica* and *F. taiwanica* differ, having 3-1-3-3 (Bayartogtokh *et al.* 2009) and the

genera *Alismobates* and *Circellobates* exhibit 3-1-2-2 (Luxton 1992; Karasawa & Aoki 2005). Further characters formerly supposed as being developed independently in this family were the presence of solenidion  $\omega_2$  on tarsus II, the existence of a lenticulus and the absence of a tutorium (Behan-Pelletier 1997). But *A. inexpectatus*, *F. atlantica* (Krisper & Schuster 2008) and *F. yunkeri* (Grandjean 1968) are lacking a second solenidion on tarsus II, a lenticulus is absent in *F. marina* (van der Hammen 1960), *F. rotunda* (Marshall & Pugh 2002) and *C. venustus* (Luxton 1992) and a tutorium is present in all *Alismobates* species and in *Circellobates* (Luxton 1992). All the above-mentioned characters are varying within the family of Fortuyniidae and can therefore no longer be viewed as characteristic for this family. On the other hand, the presence of a “van der Hammen’s Organ” (Luxton 1992), juveniles with a centrodorsal smooth area (Luxton 1992, Behan-Pelletier 1997), 14 pairs of notogastral setae and the loss of seta  $h_3$  in the larval stage (Behan-Pelletier 1997) are still constant within the Fortuyniidae and consequently remain in combination specific for the family. A further character present in all known nymphs of fortuyniid taxa (van der Hammen 1963; Luxton 1967; Bayartogtokh *et al.* 2009) is the conspicuous transverse furrow passing the genital orifice anteriorly, which may be added to the other family specific traits.

## Biogeography of Fortuyniidae

Schuster (1983, 1989) already supposed a transoceanic distribution of the family Fortuyniidae and several years later his assumption was finally confirmed when *F. atlantica* from the coasts of Bermuda was officially described (Krisper & Schuster 2008). Adding this last Atlantic record to the other known occurrences on coasts of the Indian and Pacific Ocean (Schuster 1989; Bayartogtokh *et al.* 2009), the diverse genus *Fortuynia* now exhibits a world-wide pan- and subtropic distribution. (Figure 21)

The less species rich genus *Alismobates* and the monotypic *Circellobates*, on the other hand, were found only in a very limited geographic range of the East China Sea, with records of *A. rotundus* and *C. venustus* from Hong Kong (Luxton 1992) and *A. reticulatus* from Hong Kong (Luxton 1992) and the Japanese Ryukyu Islands (Karasawa & Hiji 2004; Karasawa & Aoki 2005). The present discovery of a third *Alismobates* species on the shores of the Atlantic archipelago of Bermuda expands the geographic distribution of this genus enormously but leaves a large gap in the eastern part of the Pacific Ocean. Quite possibly further islands of the Pacific region, the Pacific as well as the Atlantic coastline of Central America and several Caribbean Islands may have been successfully colonized by this taxon but insufficient sampling within these areas may be responsible for the apparently discontinuous distribution pattern.

At present the new species *A. inexpectatus* was only recorded from the archipelago of Bermuda, but here it can be found at many localities along the coastline (Figure 22) inhabiting predominantly mats of the alga *Bostrychia tenella* growing on rocks in the littoral zone.

Although this species, as well as *F. atlantica*, may be restricted to Bermuda, their endemic status should only be regarded as provisional until the intertidal mite fauna of Central American coasts and the Caribbean Sea are investigated in a more comprehensive way and further distributions of these species can be definitely excluded.

(A sampling excursion to some of these areas will be performed by one of the authors in the near future and is supposed to give further insights into the distribution of these taxa)

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